Agency and the sense of *body*-ownership

*Psycho*physical & *Neuro*scientific Investigations

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Abstract

Almost every human activity involves voluntary bodily movements. As agents, we act upon the world with our body, and we experience ourselves, and the world through the same body. This fact implies that the sense of self is crucially dependent on motor and sensory signals. These signals are related to the phenomenological experience of agency and body-ownership. Agency is the sense of oneself as being the source of the action, the sense that actions are one's own. Body-ownership is the feeling that the body I inhabit is mine and always with me.

The sense of ownership is present not only during voluntary actions, but also during passive movement and at rest. In contrast, only voluntary actions should produce a sense of agency. Thus, agency seems to be closely linked to the generation of efferent motor signals, and ownership to the perception of afferent sensory signals. This distinction suggests that agency and ownership should have different effects on awareness of the body.

The aim of the present thesis was to investigate how efferent and afferent signals interact to generate the sense of agency and the sense of ownership. In particular, the experiments focused on four main varieties of bodily experience: time-perception, sensory-motor perception, self-recognition, and self-attribution. Overall, the results showed a consistent contribution of voluntary action to a number of different measures related to the bodily self. In particular, efference underlies the sense of agency and at the same time functions as a unifying element that structures a coherent representation of the body. At the same time, the sense of body-ownership results as an interaction between bottom-up and top-down influences: sensory inputs related to the body are integrated against a set of body-scheme representations that guarantee the functional and phenomenological coherence of bodily experience. It is suggested that the unity of bodily self-consciousness comes from action, and not from sensation.

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I dedicate my thesis to ***Όλγα*** for flying me to the moon and inviting me to write among the stars.

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Table of Contents

List of Figures

List of Tables

1. Introducing the Bodily Self

"The ego is first and foremost a bodily ego."

(Freud, 1923, 26)

The Focus of the Present Thesis

Almost every human activity involves goal-directed voluntary movements (i.e. actions). As agents, we act upon the world with our body, and at the same time we experience ourselves, and the world through the same body. Thus, the sense of self is crucially dependent on motor and sensory signals. These observations suggest that there is a functional link between the self, the action and the body. Thus, the quest to understand how the brain generates and perceives embodied actions is intrinsically linked to the emergence of a new topic in neuroscientific research: the "bodily self". The task of a cognitive neuroscience of the bodily self is to explain the sense in which percepts of action and bodily effects are so clearly and inexorably "mine".

The focus of the present thesis is to characterize the sense of agency and the sense of ownership that we experience over our actions and our bodies. These two concepts are central to the experience of the bodily self. The aim of the experiments presented in this thesis is twofold:

1. To investigate the ways in which perception of one's own body is modulated by the intentional and agentic nature of voluntary action, that is, how agency modulates body-ownership

2. To investigate the way in which multisensory signals, efferent signals and cognitive representations of the body are integrated to generate the sense of ownership over one's own body.

The experiments presented focus on four main varieties of bodily experience: time-perception, sensory-motor perception, bodily self-recognition, and self-attribution.

Outline of Chapter 1

The introduction of this thesis functions as a review of the relevant field and presents the main neuroscientific models and the empirical questions that the present thesis will address. This introductory chapter is divided in six main parts.

In part 1.1, the relationship between the self and the body is discussed. The aim of this section is to show that the study of the bodily self brings together two constitutive elements of selfhood: the physical and the psychological.

Part 1.2 focuses on the signals that constitute the operation and the experience of the bodily self. These are the efferent action-related signals, and the afferent body-related signals. These two kinds of signals are linked to the sense of agency for one's own action and the sense of ownership of one's own body. The interactions between the signals and the sense of agency and ownership are discussed with relation to recent neuroscientific models of agency.

Part 1.3 reviews the functional and neural signatures of agency.

Part 1.4 reviews the cognitive neuroscience of body-representation, and links it to body-ownership by focusing on two kinds of bodily experience: self-recognition and self-attribution.

In Part 1.5, the methodological approach of the present thesis is put forward. In particular, it is proposed that in order to study the way agency modulates body-ownership, it is necessary to systematically compare the awareness of body-related events that are self-generated, to the awareness of comparable events that are passively- or externally-generated. This can be operationalized in the distinction between the acting and sensory self.

In Part 1.6, this methodological framework is related to the specific empirical questions addressed in the experiments of the present thesis.

1.1. The Body and the Self

1.1.1. The *Experience* of Self

William James, in the chapter 'The Consciousness of Self' in the *Principles of Psychology* (1890/1981) discussed the implications of Humean empiricism and Kantian idealism for the concept of self in psychology. Interestingly, despite their philosophical differences, both Hume and Kant, though for different reasons, argued that no empirical knowledge of the self is possible.

Hume held a strong anti-self stance and in fact a "no-ownership" view, by suggesting that experiences are subject-less or ego-less: "For my part, when I enter intimately into what I call *myself*, I always stumble on some particular perception or other, of heat or cold, light or shade, love or hatred, pain or pleasure. I never can catch *myself* at any time without a perception, and never can observe any thing but a perception...[human beings] are nothing but a bundle or collection of different perceptions, which succeed each other with an inconceivable rapidity, and are in a perpetual flux and movement" (Hume 1888, p.252, italics in original). This passage seems to suggest that perceptions and experiences are subject-less, and thus the self seems to be a product of reflection or a linguistic construct (i.e. "what I call *myself*").

For Kant (1881/1996), the experience of 'being conscious of myself' has two components : (a) the empirical or psychological self, the "I" as object of consciousness, and (b) the transcendental self, the "I" as subject. The self-awareness of the empirical self arises by simply having particular experiences (e.g. taste of wine) and being aware of them. On the contrary, the self-awareness of the transcendental self requires the awareness of oneself as the subject of experience. Thus, simply being aware of a certain experience (e.g. taste of wine) would not suffice for self-awareness. Self-awareness would necessitate awareness of oneself as the one who is experiencing a certain sensation (e.g. *"I"* taste the wine). However, according to Kant, the transcendental self cannot be empirically studied, simply because I cannot know as an object that (i.e. the transcendental self) which presupposes the knowledge of any other object. Thus, every attempt to naturalize the concept of self will never reach a full understanding of its core.

It seems that Hume was too immersed into the "bundle" of (his) experiences, and thus he failed to detect the mere fact that experiences are not ego-less. Instead, experiences are always given immediately to the sensing subject from *within*, and their ownership can not be based on inference. On the other hand, the Kantian concept of self was too far away from experience itself. The transcendental self was observing the world "from above", failing, thus, to experience his own self "from within".

William James was well aware that if psychology were to abide by these philosophical doctrines, then it would run "against the entire common-sense of mankind, of which the belief in a distinct principle of selfhood seems an integral part" (James, 1890/1981, p.314). In fact, a science of selfhood is necessary not simply because human beings believe in this "distinct principle". It is precisely the phenomenological *experience* of being someone (Nagel, 1974), rather than being no one (Metzinger, 2003), that seems to be an integral part of human condition, and as such, it begs for a naturalistic explanation. According to the phenomenological tradition (Husserl, 1952/1989; Merleau-Ponty, 1962; Sartre, 1943/1976), understanding of what it means to be a self is by necessity linked to the examination of the structure of experience, and vice versa. According to phenomenology, experiences are not ego-less or subject-less. When I taste the wine, this experience is felt as mine not inferentially, but *immediately*. Thus, the empirical investigations of the self and experience have to be integrated (see also Zahavi, 2000a).

The *experience* of selfhood is constituted by two fundamental elements, the physical self and psychological self. These are not necessarily experienced separately (Merleau-Ponty, 1962), but they can be methodologically separated. The physical self corresponds to the experience of one's own body. The psychological self corresponds to the experience of one's own identity over time, but also to the experience of acting and interacting with the world. Recent approaches have used similar distinctions to approach the self (see Damasio, 1999; Dennett, 1991; Gallagher, 2000; Neisser, 1988). The great use of this almost "commonsensical" distinction lies in its applicability in neuroscientific research. Recent neuroscientific and phenomenological approaches have bridged the gap between these two aspects of selfhood, the physical and the psychological, through the systematic study of agency. Agency, here, refers to the sense of intending and executing an action (see Section 1.2.2). Thus, agency, combines the physical and the psychological

aspects of the self because it focuses on "the role of the psychological self in causing the actions of the physical self" (Gillihan & Farah, 2005, p.77). Here, the psychological self intends an action, and the physical self executes it. To that extent, cognitive neurosciences have developed the concept of embodied agency as a scientifically viable approach to investigate the psychological concept of the self.

This new approach was triggered by a radical re-conceptualization of the role of sensory and motor processes within cognition as a whole (for a review see Gallese 1999, 2000). The sensory-motor functions of the brain are no longer considered as low-level processes that are independent from higher functions such as self-awareness, agency and social cognition. For example, even from a computational point of view, the existence of an internal model of the system's own body would suffice for the evolution of an internal world model (Cruse, 2003). The consequences of the re-conceptualization of sensory-motor functions are evident in the generation of new "motor" theories of cognition and selfhood (Frith, 1992; Gallese, Keysers & Rizzolatti, 2004; O'Regan & Noë, 2001; Paillard, 1999a; Tsakiris & Haggard, 2005a), and in the formation of a new agenda of empirical research. Within this framework, recent neuroscientific research has "grounded the self in action" (Knoblich et al, 2003). Likewise, the body was now placed at the interface between the self and the world, as it became evident that sensory-motor processes can create a self-model, which can also represent the meaningful relationship between the self and the world.

1.1.2. The Bodily Self

In the present thesis, the self will be treated as the minimal sense of owning a body and the actions originating from that body (Gallagher, 2000b). This minimal self is a physical entity "which exists in a physical world and has physical effects via its physicality" (Marcel, 2003, p. 50). As such, the minimal self is predominantly a bodily self. There are several unique elements in the experience of the body that justify the link between the body and the self on one hand, and the body and the world on the other hand.

Body-presence

Contrary to the perception of an object, which can be perceived from different perspectives or even cease to be perceived, we experience "the feeling of the same old

body always there" (James, 1890/1981, p. 242). When I decide to write something, I do not need to look for my hand, in the same way that I have to look for a pen or a piece of paper. Does this permanent presence make the body special? Merleau-Ponty wrote: "[...] It is particularly true that an object is an object in so far it can be moved away from me, and ultimately disappear from my field of vision. Its presence is such that it entails a possible absence. Now the permanence of my own body is entirely different in kind [...] Its permanence is not a permanence in the world, but a permanence on my part." (Merleau-Ponty, 1962, p.90). The fact that the body is always present suggests that body-awareness is not like any other form of object-awareness, because the body is an "object" that normally never leaves *me*.

Body-perception

The body is also a unique perceptual entity by virtue of the versatile ways in which it is perceived. The body is perceived from the outside (e.g. vision), but *my* body is also perceived from the inside (e.g. proprioception, interoception). Proprioceptive sense is often conceptualized as the sense of the self *par excellence*, precisely because no one else can feel my hand moving in the same way I feel it moving from the *inside*. The fact that the body is perceived from within guarantees the immediate first-personal mode of presentation of bodily experiences. This epistemological asymmetry (i.e. no one else has access to the first-personal presentation of my bodily experiences), makes the experience of my body immune to error through misidentification (Evans, 1983; Shoemaker, 1984). In other words, when I am reaching to pick up a glass I do not question myself whether this was my hand, in the same way that I do not need to ask who is thirsty when I feel thirsty.

Body-movement

More importantly, one's own body is the only "object" in the world that can be freely moved according to one's own will. "[...] Body is an *organ of the will*, the *one and only Object* which, [...], is moveable *immediately and spontaneously* and is a means for producing a mediate spontaneous movements in other things [...] Only bodies are immediately spontaneously ("freely") moveable [...]" (Husserl, 1989, §38, pp.152, italics in original). The simple fact that we are capable of action with and sensation in our bodies is sufficient to distinguish the relation we have with our bodies from our relations with other objects (Bermúdez, Marcel & Elian, 1995).

The body and the world

Experientially, the body imposes a point of view of the world (Merleau-Ponty, 1962). It is the mere fact of embodiment that defines a certain "*point de vue*" for each embodied self, because it is thanks to the presence of the body, and its position in space that every relation between the self and the world is made possible. In that sense, the bodily self can be thought of as a "perspectival" source from where all actions emanate and to where all experiences are returned (see also Gallagher & Marcel, 1999; Marcel 2003). In addition, both the effectors that materialize our intended actions and the sensory organs that provide our perceptual experiences of the world are found in the body.

Much of human activity involves voluntary movements and sensory experiences. Both action and perception are made possible through central motor signals and peripheral sensory signals that are ever present. As agents, we act upon the world with our bodies, and at the same time we experience ourselves, and the world through the same bodies. We communicate our intentions to the world through the motor signals that are conveyed into voluntary bodily movements, and we understand the world through the interpretation of the sensory signals. Moreover, we seem to understand other people's intentional behaviour by mapping their actions onto our sensory-motor system (Gallese & Umilta, 2002). In short the body is an 'intentional arc' between the agent and the world (Merleau-Ponty, 1962), a channel of meaningful communication between the self and the world.

Having established this intimate relation between the body, the self and the world, it then becomes an empirical question to characterize the functional operation and the phenomenological experience of the bodily self. Thus, it is necessary to ask:

i. What are the signals that constitute the bodily self?

ii. What are the unique ways by which we experience the distinctive phenomenology of our bodies?

iii. What is the interaction between the signals and the phenomenal experience of the bodily self?

1.2. The Signals and the Experience of the Bodily Self

1.2.1. The Bodily Signals

The fact that the body functions as an "intentional arc" between the self and the world implies that the sense of self is critically dependent on sensory-motor signals. These signals can be classified into efferent or afferent.

1.2.1.1. Efference

Efferent signals are the centrally-generated signals that control every voluntary movement. The concept of efference copy was first described as an "effort of will" by Helmholtz in 1867 (Helmholtz, 1995). In fact, the idea of an "effort of will" was the answer to Helmholtz's question regarding our visual experience of the world: 'How is it that, when we move our eyes, the world remains stable, despite the fact that the retinal image has moved?' (see also Pachoud, 1999). In other words, how do we know whether to attribute the movement to the eye or to the object, and whether the perceived movement originates from the self or from the world? Helmholtz initially suggested that whenever we make eye movements, the "effort of will" provides critical information about the sensory outcome of the eye movement.

In the 20th century, Helmholtz's idea was further developed into the concept of an efference copy. Whenever a motor command is issued in the motor cortex, a copy of this command is generated in parallel (Sperry, 1950; Von Holst & Mittelstaedt, 1950, cited in Nelson, 1996; von Holst, 1954). This information can be used for perceptual compensation, and can help identify the source of the movement (i.e. self *vs.* other). Support for this idea comes from a very basic example: when the eye-ball is gently pushed by the finger, causing thus an involuntary eye movement, the percept of the world moves in the opposite direction of the eye movement. Thus, Von Holst and Mittelstaedt suggested that during voluntary eye movements, an efference copy can be used by visual or motor areas of the brain to predict the sensory outcome of the descending motor command, and therefore anticipate the self-generated stimulation (i.e. the sensory feedback originating from the eye movement). However, the efference copy and the sensory feedback cannot be simply compared, because the efference copy is in effect a motor command (Merfeld, 2001). Thus, the efference copy needs to be translated to appropriate coordinates that can be compared to sensory signals. Once the efference

copy is translated into sensory coordinates, the impending sensory feedback can be predicted and then compared to the actual sensory feedback. The outcome of this comparison, called "corollary discharge" (Sperry, 1950; see also Nelson, 1996), signals the presence or absence of a discrepancy between the predicted and the actual feedback originating from the saccadic movement. In the absence of any discrepancy, the world continues to be perceived as stable. More recently, the idea of an efference copy has been generalised to the operation of the motor system, and it is not restricted only to the operation of occulomotor system. Thus, an efference copy is thought to be generated whenever a motor command that precedes a *self*-generated movement is issued.

1.2.1.2. Afference

Afferent are the sensory peripheral signals that can be either the effect of self-generated stimulation (re-afferent) or of externally-generated stimulation (ex-afferent). The afferent peripheral signals seem to support an ecological self-awareness (Gibson, 1979), in the sense that they provide information about the body, but this information is not perceived in isolation from the environment. According to Gibson each act of perception contains both propriospecific information about the self, as well as exterospecific information about the distal environment: "Egoreception accompanies exteroception, like the other side of the coin....One perceives the environment and coperceives oneself" (Gibson, 1979, p.126). This statement is the physiological counterpart of the philosophical statement that the experience of the body is at the interface between internal and external milieu. Afference, and especially proprioception, provides us with the phenomenal content of our bodily self-awareness, because proprioceptive information unambiguously pertains to the self. However, the meaning of afferent signals for perception and behaviour is ambiguous, precisely because the afferent signals can be either self- or externally-generated (see Section 1.2.2.3).

We do not normally experience the efferent and afferent components separately. Instead, we have a general awareness of our bodily actions that involves both components. However, the efferent and the afferent signals may support different functions, and may give rise to distinct forms of body-awareness. In fact, recent neuroscientific and phenomenological approaches to selfhood (Bermúdez, Marcel & Eilan, 1995; Kircher & David, 2003; Zahavi, 2003) distinguish between two aspects of bodily self consciousness: the sense of agency and sense of ownership.

1.2.2. The Sense of Agency and the Sense of Body-ownership

1.2.2.1. Operational definitions of Agency and Body-ownership

Sense of Agency

Sense of agency is the sense of intending and executing an action (Gallagher, 2000a,b)), a sense of oneself as an actor or a sense that one's actions are one's own (Marcel, 2003). In agency, the self is experienced as the source of the experience of the acting, suggesting that the relationship between the self and the action is not simply causal, because that would imply that the agent can be separated from the action. Instead, the actor experiences herself as the source of doings, because she is immersed in her activity of doing. This stance implicitly suggests that awareness of action cannot be separated from agency, at least not under normal circumstances. On one view, "awareness of action that happens to be one's own may carry with it, intrinsically or extrinsically, its ownership" (Marcel, 2003, 54). This may be true to the extent that the awareness of our own bodily actions is special. It has been suggested that there is a special kind of knowing that applies only to oneself, such as knowledge of thoughts, intentions and desires. These kinds of awareness are non-inferential and non-observational, and may also support awareness of action, and as such they may specify the source of the action.

Sense of Body-ownership

The feeling that the body I inhabit is mine and always with me is called body-ownership. This feeling is a fundamental element of the phenomenal experience of my body. Moreover, ownership refers to the sense that "I" am the experiencing subject, my body is the site where the sensory experience takes place, and it is my body the one that experiences a certain sensation, either self- or externally-generated (see also Gallagher, 2000b). Thus, the sense of body-ownership is present when I move voluntarily, but also when an externally-generated somatic sensation is experienced by me, and also when my body is at rest. The raw basis of body-ownership is provided by (a) the epistemologically private experience and knowledge that I have of my body from *within* (e.g. as provided by the proprioceptive sense) , (b) the body schematic control of movement, and (c) the pragmatic differentiation between self and non-self that is the direct consequence of embodiment (see also Bermúdez, 1998; Gallagher, 2003). Thus, body-ownership seems

to support a non-conceptual and pre-linguistic form of self-awareness, which is ontogenetically more primitive than the higher form of reflectional self-consciousness (Bermúdez, 1998; Zahavi, 2002). Developmental psychology suggests that an implicit awareness of the body is present even at birth. 24-h-old infants are able to discriminate between self-originated and externally-originated tactile events (Rochat & Hespos, 1997; for a review see Rochat, 2003). Thus, body-ownership may have an important psychological consequence in distinguishing between self and others on the basis of embodiment.

Following these operational definitions, the sense of agency involves a strong efferent component, because actions are centrally generated. On the other hand, the sense of ownership involves a strong afferent component, because the content of body-awareness originates mostly from the plurality of multisensory peripheral signals. An important phenomenological observation is that the sense of ownership is present not only during voluntary actions, but also during externally- or passively generated experiences. In contrast, only voluntary actions, or actions that are experienced as voluntary, should produce a sense of agency. To give an example, when I voluntarily move my hand, I have a sense of agency by identifying *my intention* to move as the source of the movement, and a sense of ownership, by identifying the moving hand as *mine*. However, if someone else moves my hand, I do not have a sense of agency over the hand movement, yet I retain a sense of ownership of the moving hand as being *mine*. The interaction between the sense of agency and body-ownership becomes apparent in cases of abnormal action- and/or body-awareness.

1.2.2.2. Disorders of agency

One fundamental assumption of cognitive neuroscience is that the way we behave and the way we experience the world is determined by the way our brains work. Thus, pathological cases may provide useful insights about the neuroscientific theories of normal functioning. Two examples taken from the psychiatric and the neurological literature may be used to illustrate how brain processes underpin the sense of agency and body-ownership in normal experience.

Schizophrenic patients with delusions of control demonstrate a striking failure to experience their own agency over the actions that they execute (Schneider, 1959; Frith, 1992). The delusion of control is an example of a passivity experience in which a patient

feels that his own actions are being created, not by himself, but by an outside force, usually an external agent. Increased activation in the right parietal cortex was related to the experience of passivity phenomena in schizophrenic patients (Spence et al., 1997).The delusions of control can occur even for simple actions, such as picking up an object, but also for more complex behaviours such as thought or speech production. The main feature of this symptom is that the intention to act is mis-attributed to another agent, whereas the ownership of the body-part that executes the action is not. That is, in phenomenological terms, the body is moving, but the source of its movement is not "me". It is precisely the feeling that things happen in a patient's *own* mind and body, without her having any control (i.e. agency) over these experiences that is pathological and distressing for the patient.

Another example, that illustrates the complex interaction between agency and ownership, is taken form the neurological literature on the Anarchic Hand Syndrome. The Anarchic Hand Syndrome is usually associated with damage to the supplementary motor area and/or the anterior corpus callosum (Della Sala, Marchetti & Spinnler, 1994). The main symptom is related to the behaviour of the hand contralateral to the lesion. The contralateral hand performs simple, goal-directed movements which are not intended by the patient. In that sense, the behaviour of the contralateral hand is thought to be anarchic. For example, Della Sala, Marchetti and Spinnler (1991) described a patient who exhibited a right anarchic hand following a combined callosal and mesial frontal lesion. When the patient was offered a cup of tea, she said that she would not drink it right away, and that she would wait a while until it cooled. However, her right "anarchic" hand "ignored" her conscious intention to wait, and moved in a goal-directed way to reach and pick up the cup. Eventually the patient had to restrain the anarchic hand with her left, unaffected hand. Despite the autonomous behaviour of the affected hand, these patients retain a sense of ownership of the moving hand. In phenomenological terms, it is certain actions performed by the contralateral hand that are disowned, and not the hand itself (see also Marcel, 2003).

In schizophrenia, as well as in the anarchic hand syndrome, there is a breakdown in the normal experience of agency (Frith, Blakemore & Wolpert, 2000a,b; Frith, 2005). In both cases, the authorship of the action cannot be traced back to the self: the source of the action is not the agentic self. Moreover, a sense of body-ownership for the executed

movement seems to be present in both cases. However, there is a clear difference between the two conditions. Schizophrenic patients misattribute the intention to an external agent. In a rather different way, patients with anarchic hand syndrome do not experience any delusion of control, since the intention to act is not misattributed to an external agent, but it is attributed to the anarchic hand itself. The sense of agency is affected in both cases since the action is dis-owned, yet the deficit differs: the hand of the schizophrenic is acting according to the will of an external agent, whereas the anarchic hand has a will of its own (see also Marcel, 2003).

On one view, the delusions of control arise as a result of an abnormal awareness of the initiation of the action or of the predicted consequences of this action, whereas in the anarchic hand syndrome the deficit lies in the control of the action (Blakemore, Wolpert & Frith, 2002). Clearly, in both cases, the patients are aware of the action they disown. Otherwise, they would not be able to experience and report the action as dis-owned. How is this possible? Marcel (2003) suggests that, at least the patients with anarchic hand are aware of the action they disown by virtue of the proprioceptive signals. It may be argued that the same is true for schizophrenics. In fact, according to Frith and Blakemore, schizophrenics seem to be excessively aware of afferent events (Blakemore et al., 2000; for a review see Frith, 2005). If this is true, then in the normal experience of agency, awareness *and* ownership of action should also involve signals that precede the afferent feedback, that is, signals that are related to the generation of the action. For both schizophrenic patients and patients with anarchic hand, the actions are not experienced from *within*, but they are observed as if they happen outside the self. Thus, the cognitive neuroscience of normal agency has to answer how a non-observational knowledge of one's own actions can be implemented in neural and functional terms, and can give rise to the sense that actions originate "within me". The two clinical examples described above illustrate the complex interaction between the experience of agency and body-ownership. Moreover, these two examples suggest that efferent and afferent information play important roles for the normal experience of the bodily self.

Even though, efferent and afferent information jointly constitute the core of our bodily self-awareness (Bermúdez, Marcel & Eilan, 1998), their respective contributions to different aspects of action- and body-awareness are still under ongoing research. In effect, a long-standing debate regarding the influence of efferent and afferent

information on action-awareness started more than 100 years ago. In the "Williams debate" (see Petit, 1999), William James argued that knowledge of our movements originates from peripheral information, whereas Wilhelm Wundt emphasised the role of central motor signals. Both these sources may produce distinctive phenomenologies of bodily experience. Although the "Williams debate" originally concerned the representation of actions, it has wider implications: is the "bodily self" primarily an afferent experience of our bodies, or primarily a motor experience of our bodily actions? This question cuts across the whole field within which the present thesis is situated.

1.2.2.3, Ambiguity of afference and the motor system

A first approach to the question regarding the motor and proprioceptive experience of our bodies is to focus on the interaction between efferent and afferent signals. This interaction can be exemplified in the ambiguity of afferent information. Afference results from either self-generated actions (i.e. as a result of efferent signals) or as a result of externally-generated sensory stimulation. Therefore, the meaning of afferent information for perception and behaviour is ambiguous. Recent theories of motor control have shown how an interaction between efferent commands and sensory inflow may reduce this ambiguity.

In the case of a self-generated action, intentions and efferent information can predict the consequent multisensory signals produced by one's own movement (Helmholtz, 1995; Sperry, 1950; von Holst & Mittelstaedt, 1950; Wolpert 1997). This prediction takes place in the internal models of the motor system. Figure 1-1 shows a model of the motor control system put forward by Blakemore, Wolpert and Frith (2002). This model shows the relationship between motor commands and sensory feedback and it postulates several kinds of additional variables or motor representations called state variables.

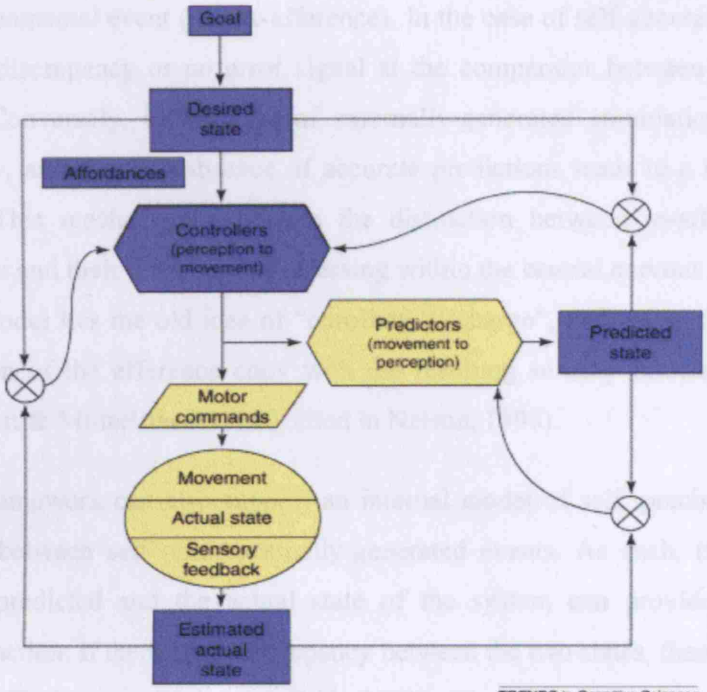

Figure 1-1 A framework of the motor control system (Blakemore, Wolpert & Frith, 2002). Motor representations coloured in mauve are available to awareness, whereas the ones in yellow are not.

The desired state refers to representation of the goal of the action. An internal model of the motor system called the "inverse" model or controller generates the appropriate motor commands that are necessary for the achievement of the goal. The efference copy of the motor command is processed by another internal "forward" model or predictor, which predicts the sensory outcome of the movement.

There are two kinds of forward models. The forward dynamic model compares the intended and the predicted outcome. Thus, the forward dynamic model makes predictions about the next state of the system and compares this with the desired state, allowing thus for rapid on-line correction of errors. It is therefore particularly useful for motor learning. The forward output model makes predictions about the sensory consequences of the movement, and this prediction is compared with the actual sensory consequences of a movement. For the purposes of the thesis, the use of the term forward model refers to the forward output model.

The predicted state of the system calculated by the forward model is turn compared to the estimated actual state that includes the sensory feedback. The sensory

feedback is the sensory consequence of the movement itself (i.e. re-afference), plus any relevant environmental event (i.e. ex-afference). In the case of self-generated movement, there is little discrepancy or no error signal at the comparator between predicted and actual state. Conversely, in the case of externally-generated stimulation, there is no efference copy, and thus the absence of accurate predictions leads to a higher sensory discrepancy. This mechanism facilitates the distinction between re-afferent and ex-afferent signals and their differential processing within the central nervous system. At the core of this model lies the old idea of "corollary discharge", defined as the outcome of the comparison of the efference copy with the resulting sensory information (Sperry, 1950; von Holst & Mitterlstaedt, 1950, cited in Nelson, 1996).

The framework can also support an internal model of self, precisely because it distinguishes between self- and externally-generated events. As such, the comparator between the predicted and the actual state of the system can provide an index of authorship of action: if there is no discrepancy between the two states, then the event was self-generated (Blakemore, Wolpert & Frith, 2002). Thus, the ambiguity of afference for the bodily self seems to be resolved by the generation of an efference copy and the processing of this efference copy within the motor system. However, it remains unclear whether and how the internal motor processing would be sufficient for the generation of the conscious sense of agency. Whereas this model can account for the "error awareness" that we have when unexpectedly the effects of our actions do not match our intentions, it does not explain how the absence of a mismatch at the level of the comparator could generate the conscious experience of agency. It is logical to suppose that the main function of the comparator is to generate error signals, which can then be used to modify the behaviour. In that sense, "no error" signals do not need to enter consciousness, because the events occur as predicted.

1.2.3. Models of Agency

The predictive function of the motor system has been well documented in the literature across different experimental paradigms (for a review see Davidson & Wolpert, 2003). However, the link between the operation of the internal models of the motor system and the conscious experience of action and its effects is still debated. A critical issue in this debate relates to the question of the conscious experience of agency.

It is not clear which signal(s) or state variable(s) of the motor system give rise to the conscious experience of agency. Accumulating evidence suggests that we are not aware of the actual motor commands or motor parameters of our actions (see for example Bridgeman, Kirch & Sperling, 1981; Goodale, Pélisson & Prablanc, 1986; for a review see Jeannerod, 1997). This un-awareness of the actual motor commands was nicely demonstrated by Fourneret and Jeannerod (1998) in a replication of the original experiment by Nielsen on volition (1963). Participants were asked to draw lines in a sagittal direction on a digital tablet using a stylus. When tracing a line on the tablet, the subjects could see through the mirror a red line appearing on the computer screen in exact coincidence with the displacements of the tip of the stylus on the tablet. The output of the graphic tablet was processed by the computer using a simple algorithm for adding a linear directional bias. When the bias was set to the right (e.g. at 15°), a line traced in the sagittal direction on the tablet appeared to the subject to deviate to the right at an identical angle. Subjects were able to correct for the introduced bias, and managed to trace lines that appeared to be sagittal. However, when asked after each trial to either report verbally their movement or to reproduce it, it became evident that they were unaware of the corrections they produced during the experimental trials. This finding suggests that they were not able to consciously monitor the signals generated during their movements.

A theoretical implication of this study is that there seems to be a two-level coding of action-related information (see Georgieff & Jeannerod, 1998). The 1st level codes the sensory and motor signals that are used for the control and monitoring of movements. These signals are not made available to consciousness, and therefore they are not the ones used for conscious judgments of actions. According to Georgieff and Jeannerod (1998), the 2nd level coding of action-related information represents the "public" aspects

of action (see also Frith, 1995), whereas the 1st level represents the "private" aspects, such as the efference copy, the motor command, and the sensory feedback. The 2nd level is only necessary if we take a public view of action.

The public view of action-representations is based on the ideomotor theory put forward by James (1890, 1981). The basic hypothesis of the ideomotor approach is that actions are coded in terms of the perceptual events resulting from them. Therefore, in action generation, the actual movement is governed by a representation of the goal of the action, which is agent-neutral. Similarly, in action perception, the generated representations attempt to detect the intended goal. Thus, both own and other's people actions are coded in a common way (see the common coding theory, Prinz, 1997). Similarly, perceived events (i.e. perceptions) and to-be-produced events (i.e. actions) are commonly represented by an integrated network of cognitive structures called event-codes (for a review see Hommel et al., 2001).

With regards to the issue of agency, according to the common coding theory, there are neither quantitative nor qualitative differences in the generation and processing of these common representations that would enable the *a priori* attribution of the source of the action (i.e. agency). Knoblich and Flach (2001), in an experiment on action prediction, where participants had to predict the outcome of either self- or other-generated actions (e.g. throwing darts), found an authorship effect in correctly predicting the outcome of self-generated actions. In the light of this evidence, they acknowledge that one problem paused by the common coding theory is that "[...] first-person and third-person information cannot be distinguished on a common-coding level" (Knoblich & Flach, 2001, p. 468), and they interpreted their results by adopting the model of "intentional schemas" (Barresi & Moore, 1996). At the core of the "intentional schemas" lies the presumption that different types of intentional schemas enable us to link first-person and third-person information more flexibly. On that view, the authorship effect reported by Knoblich and Flach could be accounted by the fact that the motor system that perceived the action during the prediction task was the same motor system that generated the action. Thus, the matching process between first-person perspective (i.e. producing the effect) and third-person perspective (i.e. observing the effect) was even more complete, leading to more accurate predictions (for a review see Knoblich & Flach,

2003). Nevertheless, it remains unclear what could be the functional role of the first-person perceptive in action generation and perception:

> "In any case, we see no indication of privileged access to 1st person knowledge, that is, to knowledge referring to the mental preparation of the upcoming action and arising before the fact. Rather, like any other event, both the physical action itself and its mental antecedents appear to be perceived *after* the fact. The mental representation seems to follow the physical event it represents." (Prinz, 1997, 149, italics added).

According to the public view of action-generation and perception, agency of action is not intrinsically embedded in the generation of the action. Instead, agency of action is the result of an attribution process that takes place at the observational level of public aspects of action that happen after the action *itself*. In neuroscientific terms, the problem of agency becomes a question of whether agency is a correlate of post-action, action-related, or pre-action neural processing. In other words, is agency invented, inferred, or experienced? The review that follows focuses on the information-processing implications of three recent theoretical frameworks of agency.

1.2.4.1. Post-action processing and agency

Jeannerod and colleagues (de Vignemont & Fourneret, 2004; Georgieff & Jeannerod, 1998) have argued for the necessity of a specialized neural system that would discriminate between the self and the other, and thus provide the sense of agency. The function of this "who system" is to answer the question "who made the action?". The necessity of the "who system" is justified by the fact that several kinds of action representations are independent of the agent who is performing them. It has been shown that both the representations of self-generated and observed actions activate overlapping neural networks (for a review Grèzes & Decety, 2001). These common activations "share" representations of actions that are agent neutral (Jeannerod, 2003a,b). According to the "shared representations" model, the "who did it?" question can be answered in computational terms only by disentangling the non-over-lapping areas that are active during self- and other-actions. Neither the intention of the acting subject, nor the translation of the intention into an efference copy and a motor command suffice for the experience of agency. Within this framework, even intentions seem to be agent-neutral:

"It could be the case either that intentions [...] are impersonal representations or that, although their form is <agent, action, goal>, the agent parameter can be left unspecified" (Jeannerod and Pacherie, 2004, p.139). Thus, for the "who system", the default mode of operation seems to be "no agent". This line of argument implies that the sense of agency arises as a post-action reconstructive meta-representation.

The "who system" seems to be strongly committed to a representational model of agency and self-consciousness, and thus, the problem is no more that of *being* the agent, but it is rather that of *knowing* who the agent is. In this sense, the model ignores all the processes that precede the execution of intentional actions, and instead focuses on the perception of action as an objective manifestation of "naked intentions" (Jeannerod & Pacherie, 2004). However, the acting body is perceived, not only from the outside (e.g. vision), but also from within (e.g. proprioception), and it is therefore experienced in an epistemologically immediate fashion. Moreover, efferent signals are present only when an action is self-generated, and thus, they could in principle code in an intrinsic way the origin of the action. In effect, the "shared representations" model and the "who system" raise an epistemological problem, because they leave no room for a phenomenally or epistemologically special self. If "shared representations" is the brain's basic model, then the "who system" is needed in order to reconstruct the representation of an agentic self.

However, agency requires a subjective point of view (Zahavi, 1999).By refuting the very possibility of an intrinsic link between intention, efference and action, it is impossible to provide an ecological conceptualization of agency. The consequence of such a doctrine is that conscious agency can only be "the mind's best trick" (Wenger, 2003); an "after the fact", perhaps illusory, ownership of the intention to move (Wegner & Wheatley, 1999). However, it may be possible that the sense of agency is a phenomenological correlate of a neural or functional signature that is unique to voluntary actions. On this hypothesis, agency is not embedded in the public aspects of action, but may arise as an intrinsic property of action-execution or even action-generation processes (see Haggard, Aschersleben, Gehrke & Prinz, 2002; Haggard & Clark, 2003).

1.2.4.2. Action-related processing and agency

One important aspect of agency involves the ability to distinguish actions and effects that are self-generated from those generated by another agent (Blakemore, Wolpert & Frith, 2002; Blakemore & Frith, 2003). The ability to distinguish between

self-generated and externally-generated events is embedded in the function of the motor system. As aforementioned, in the case of a self-generated action, intentions and efference copy predict the consequent visual, auditory and somatosensory signals produced by our movements. It has been postulated that a central monitor (Frith, 1992) or an internal "forward model" (Wolpert, 1997) serves this function. The role of the forward model is twofold. First, the prediction is needed to anticipate and compensate for the sensory effects of movement. Second, the forward model is used to filter the incoming sensory stimulation, by attenuating the re-afference and thus discriminating between re-afference and ex-afference. The filtering process can be used to discriminate between self-generated and externally-generated actions and effects.

The forward model of the motor system receives the efference copy of the motor command. Within the forward model, the efference copy is transformed into sensory coordinates, and in turn, the model uses these coordinates to generate predictions about the expected sensory feedback. Once, the actual sensory feedback arrives, it is compared to the prediction. If the actual feedback matches the predicted one, then the prediction can be used to cancel out the re-afference by attenuating it (Blakemore, Frith & Wolpert, 1999). Thus, when no mismatch is detected, the action is attributed to the self because the sensory feedback is recognized as being self-generated.

One important application of this "comparator" model of agency is that it can account for the phenomenology of the schizophrenic symptom of passivity. Schizophrenic patients with delusions of control often experience that their actions are not intended by them, but instead they are intended by an external agent who is actually using their bodies to perform them. Thus, whereas their movements are normally generated in physiological terms, they fail to perceive them as being self-generated. One hypothesis of the "comparator" model of agency is that these patients fail to successfully discriminate between self- and externally-generated afferent events. Thus, one possible cause of the delusional symptom could lie in the abnormal operation of the comparator. This account predicts that schizophrenic patients should not show sensory attenuation for self-generated sensory events, because these events are not accurately predicted. In fact, this hypothesis has been confirmed in a series of experiments (e.g. Blakemore et al., 2000, for a review see Frith, Blakemore & Wolpert, 2000b).

The forward model postulates that awareness of initiation of the movement has to wait until the predictors have successfully specified the sensory consequences of the movement (Frith, Blakemore & Wolpert, 2000a). However, the model implicitly assumes that agency ascription is not possible until the sensory feedback can be compared to the prediction. In other words, action is not intrinsically self-*owned* from the very moment of its initiation, but on the contrary, is verified as one's own action on the basis of the available predicted and actual sensory feedback.

Interestingly, even though the focus of this model is on processes that are action-related, it emphasizes the sensory prediction based on the motor command, while it does not explicitly test the hypothesis that efferent information *per se* could support the self-other distinction. In other words, why should a pragmatic or executive function of the motor system that is present only in the case of a self-generated action (i.e. the efference copy), be less important than a verificational function (i.e. the comparison) for the identification of the origin of the action?

1.2.4.3. Pre-action processing and agency

The hypothesis that awareness of action and agency is based on pre-action neural processes is supported by the investigation of time-awareness of action. In Libet's experiment (Libet et al., 1983b, Libet, 1985), participants watched a clock hand on a monitor rotating with a period of 2560 milliseconds (ms), and they were asked to make a simple manual movement at a time of their own choice. Their task was to report retrospectively the time at which they first "felt the urge" to make the movement (**W**ill judgment), or the time that they actually moved (**M**ovement judgment). Participants' W judgments preceded the onset of muscle activity by an average of 206ms, while M judgments preceded the onset of movement by an average of 86 ms. The readiness potential (RP) started at about 700ms before the onset of movement as measured by electromyography (EMG). Thus, the participants became aware of their intention to move after the brain begun the process of initiating the action (i.e. LP). Moreover, the participants became aware of their actual movement before they actually moved, and long before any sensory feedback reached the cortex. This suggests that awareness of action initiation is anticipatory, and that at least the initial awareness of action is based on the motor command and not on the sensory feedback.

However, it must be emphasized that the participants reported these judgments after the movement itself. Post-action processes can "reposition" awareness of action to an earlier time (Dennett & Kinsbourne, 1992). Therefore, in the original Libet study there is no clear evidence suggesting that the anticipatory awareness of action reflects a genuine consequence of discreet neural processing, and that it is not simply a reconstruction. One way to control for this confound is to interfere at the level of the neural processes that support action generation and examine the effects of this manipulation on the behavioural data.

One such approach was reported by Haggard and Magno (1999). They asked the participants to react to an auditory stimulus by pressing a response key, and then to judge the perceived time of the onset of their reaction by using the Libet method. Transcranial magnetic stimulation (TMS) was delivered either over the primary motor cortex (M1) or over the supplementary motor area (SMA), 75 ms before each subject's median reaction time. TMS over M1 produced significant delays in their actual reaction time (RT), but much smaller delays in the perceived onset of their reaction (judged RT). Conversely, TMS over SMA produced smaller delays in actual RT and relatively larger delays in judged RT. Thus, TMS over the SMA specifically affected the awareness of movement, without affecting the actual motor performance. This study suggests that awareness of action is related to neural processes implemented in areas upstream of M1. Thus, awareness of action is not a post-action reconstruction, but instead it reflects the distinct pre-action neural processing that underpins action generation.

In another experiment, Haggard and Eimer (1999) investigated whether awareness of intention and action is related to specific or non-specific motor processes. Action plans begin as non-specific and become increasingly specified as they are developed for execution. In the experiment by Haggard and Eimer, participants were asked to perform simple voluntary movements with either their left or right index finger at the time of their own free choice. They were instructed to judge the onset of the initiation of movement ("when they first began to prepare the movement", **W**ill judgment) or the onset of the movement (**M**ovement judgment). Their W judgments covaried with the onset of the Lateralized Readiness Potential (LRP), which is a specific signal of the chosen motor preparation, and not with the Readiness Potential (RP), which reflects general preparation for action. The LRP onset occurred significantly earlier on

trials with early awareness of movement initiation (W judgment) than on trials with late awareness of movement initiation. The opposite correlation was found for the RP. Thus, awareness of intention is correlated to the neural processes of specification of the motor programme.

These experiments suggest that the sense of agency may be supported by action-related signals that precede the onset of the action itself. The study by Haggard and Magno (1999) showed that awareness of responses is generated, at least in part, between premotor areas affected by stimulation over the SMA and the primary motor cortex, supporting the hypothesis that awareness of action is linked to pre-action rather than post-action reconstructive processes. The study by Haggard and Eimer (1999) showed that initial awareness of movement derives from pre-action processes of movement specification. Taken together, the cognitive neuroscience of time-awareness of action supports the hypothesis that agency may be specified at the level between the formation of an intention and its translation to a motor command. However, these experiments focused on one dimension of agentic behaviour, namely the generation of action, while ignoring another important dimension, namely the fact that actions produce effects.

Summary

The neuroscientific models of agency presented in this section can be distinguished according to whether they are committed to a re-constructive or a constructive view of agency. The "who system" suggests that agency is a post-action inference, and this does not exclude the possibility that, under certain circumstances, agency may also be "invented". In other terms, agency may be a reconstructive illusion that is not linked to any intrinsic property of the action itself. On the contrary, the comparator model of agency and the neuroscience of time-awareness of action are committed to the study of the intrinsic properties of agentic actions that are embedded in the operation of the motor system. If agentic actions are indeed characterized by unique functional and neural signatures, then it would be difficult to suggest that agency could arise as a reconstructive inference. The presence of such signatures would favour the view that agency is an on-line experience of action-generation. The literature on the functional and neural signatures of agency is reviewed in the next section.

1.3. Towards a neuroscientific understanding of agency

1.3.1. Functional Signatures of Agency

The functional signatures of agency refer to two critical components of voluntary actions: (i) the distinctive temporal structure of actions at the neural and phenomenal level, and (ii) the way these actions structure the perception of their effects.

1.3.1.1. Intentional binding

Consciousness has a temporal structure which is one of the fundamental characteristics of the experience of the self and the world (Husserl, 1964; James, 1890/1981). Moreover, consciousness involves an experience of time that is not properly ordered to objective time, suggesting that phenomenological time does not match perfectly with real time (Libet et al., 1983; Libet, 1991; Haggard, 2005a,b). In this context, time-awareness of action refers to the perceived time of actions and their sensory effects (Haggard et. al, 2002). Voluntary embodied actions have a distinctive temporal structure: from the generation of intention and its 'translation' to a motor command and the accompanying efference copy, to the execution of the movement and perception of the effects. Time-awareness of action is one critical dimension of agency, not only because actions are temporally structured, but also because intention is principally "a property of action, an action whose end is *anticipated*" (Pachoud, 1999, p.197, italics added). Therefore the temporal consciousness of the bodily self in action may constitute a unique functional signature underlying the phenomenal experience of agency.

As shown in section 1.2.4.3, the neuroscience of time-awareness (Libet et al., 1983b; Haggard & Eimer, 1999; Haggard & Magno, 1999) suggests that pre-motor processes support the initial awareness of action. Another conclusion, that has often been neglected, can be drawn from these studies. The time difference between the conscious experience of intending an action (W judgment) and the conscious experience of execution of an action (M judgement) is restricted to a compressed time-window of approximately 120ms. Given that the corresponding neural activity, from RP onset to muscle activity extends over a much longer period (~700ms), the subjective experience of intentional action seems to be temporally compressed relative to the underlying neural events (Frith, 2002; Haggard, 2005a).

The observations that our action awareness seems to be based on predicted rather than on actual sensations (Haggard & Eimer, 1999; Haggard & Magno, 1999), and that the brain links together the various components and events of the action may reflect a common phenomenon: conscious awareness of intention and action represent a compressed time-scale, which does not match the neural time-scale of these events, nor the actual time-scale of the events as they occur. A similar mechanism might underlie the time-awareness of the actions and its effects. In fact, investigation of the time-awareness of actions and their effects (Haggard et. al., 2002), rather than that of intentions, might be a more viable research topic for three main reasons. First, both actions and their effects, but not intentions, occur at an independently measurable point in time, and thus, the correlation between subjective and objective time is made possible. Second, actions and effects can be self-generated or externally-generated, and thus, we can investigate the effect of agency on time-awareness, by comparing the perceived times of self-generated vs. externally-generated events. Moreover, studying the perceived time of voluntary actions offers an indirect way of studying intentions, by comparing awareness of intentional movements with awareness of physically identical movements, which are non-intended.

Haggard, Clark and Kalogeras (2002) used a modified version of the Libet method (Libet et. al, 1983b) to investigate the relationship between time-awareness of actions and effects. Subjects were asked to judge the time-onset of (a) a voluntary key-press, (b) an involuntary movement (i.e. TMS-induced flexion of the index finger), or (c) an auditory tone. In the baseline conditions, only one of these events occurred in each trial, and subjects judged the time-onset of this event by using the Libet method (Libet et al., 1983b). In the operant conditions, the events were combined, so that a voluntary movement produced the auditory tone 250ms later, or alternatively, the tone followed 250ms after the onset of the involuntary movement. A sham-TMS condition was also used as control. In different conditions, subjects judged the onset of any of these events. Figure 1-2 shows the mean perceptual shifts across conditions.

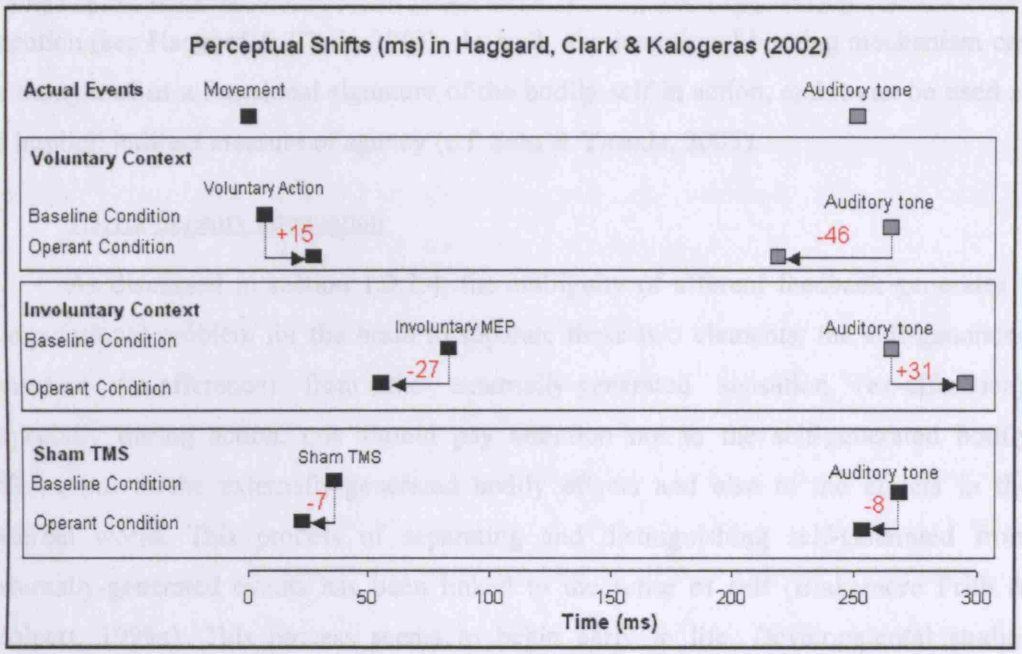

Figure 1-2 Mean perceptual shifts (in red) across conditions in Haggard, Clark & Kalogeras (2002). To calculate the mean perceptual shifts, the judgments obtained in the single-event conditions (i.e. each event occurred on its own) were subtracted from the judgments obtained in the operant conditions (i.e. a voluntary or a TMS-induced movements followed by an auditory stimulus)

Participants perceived voluntary movements as occurring later and their sensory consequences as occurring earlier than they really did, when these events occurred together compared to when they occurred in isolation. Approximately comparable involuntary movements caused by TMS over the motor cortex reversed this attraction effect between the movement and the auditory tones, producing a perceptual repulsion in the opposite direction. Haggard, Clark and Kalogeras (2002) concluded that only truly operant intentional actions, that is actions that produce an effect, elicit perceptual attraction or binding effects between the action and its sensory auditory consequence.

These results suggest that the volitional character of the movement modulates not only the time-perception of the action, but also the perception of the sensory stimulus following that action. Awareness of actions and effects showed an attraction in time towards each other, termed "intentional binding" (Haggard, Clark & Kalogeras, 2002). This effect seems to be a specific construction of the mind that is broadly associationist, and unique to intentional operant actions, that is, actions that cause an effect. Moreover, for binding to occur, the prior presence of an intention is required, but that may not be

sufficient: an intention has to be directly linked to the action that realizes this particular intention (see Haggard & Clark, 2003). As such, the intentional binding mechanism can be thought of as a functional signature of the bodily self in action, and it can be used as an implicit indirect measure of agency (c.f. Sato & Yasuda, 2005).

1.3.1.2 Sensory attenuation

As discussed in section 1.2.2.4, the ambiguity of afferent feedback generates a computational problem for the brain to separate these two elements: the self-generated sensation (re-afference) from the externally-generated sensation (ex-afference). Especially during action, one should pay attention not to the self-generated bodily effects, but to the externally-generated bodily effects and also to the effects in the external world. This process of separating and distinguishing self-generated from externally-generated events has been linked to the sense of self (Blakemore Frith & Wolpert, 1999a). This process seems to begin early in life. Developmental studies showed that newborn infants (24 hours old) are able to discriminate between double touch stimulation combined with proprioception, and single touch of exogenous origin (Rochat & Hespos, 1997).

The phenomenon of sensory attenuation has become a key concept in recent accounts of the link between perception and action, because it highlights the way that perception of sensory events is modulated by the voluntary nature of the movement. Blakemore and colleagues (Blakemore, Frith & Wolpert, 1999; Blakemore, Goodbody & Wolpert, 1998; Blakemore, Wolpert & Frith, 1998), following Weiskrantz's idea (Weiskrantz et al., 1971), investigated in detail the way somatosensory consequences of our own actions are perceived differently from identical somatosensory inputs that are externally generated. In one study by Blakemore and colleagues (Blakemore, Frith & Wolpert, 1999), tactile stimulation was applied on the participant's right hand. The stimulation was either produced by a voluntary movement of the participant's left hand, or it was externally generated. Crucially, for the self-generated condition, a robotic interface mediated between the movement of the left hand and the stimulated right hand, so that the experimenters could manipulate and parametrically vary (a) the delay between movement and stimulation, and (b) the degrees of trajectory perturbations. Participants perceived the tactile stimulation as significantly less ticklish when it was self-generated, compared to the externally-generated condition, suggesting that relevant perceptual

attributes of stimulation were attenuated. When a time delay of 200ms was artificially introduced between the self-generated movement and the resulting sensation, the attenuation effect was absorbed. Similarly, the perceived tickliness increased significantly with increasing trajectory perturbation. Therefore, even in the case of self-generated stimulation, the tactile sensation and its causative movement should correspond in time and space, for the attenuation to take place.

Neuroimaging studies on sensory attenuation, showed decreased activation in the cerebellum and secondary somatosensory cortex during self-generated movements that led to sensory stimulation (Blakemore, Wolpert & Frith, 1998). Activity in the cerebellum increased as the discrepancy between the predicted and actual feedback increased. This suggests that the cerebellum is involved in the comparison between predicted and actual sensory feedback (Blakemore, Frith & Wolpert, 2001), and that it provides the signal used for sensory attenuation in the somatosensory cortex (Blakemore, Wolpert & Frith, 1998, 1999).

The reasons for sensory attenuation are probably twofold. First, any body movement potentially increases the amount of afferent information to the brain. Sensory attenuation would reduce the possibility of computational overload. Second, the sensory consequences of self-generated actions can be predicted internally, so there is no need to sense them. The forward model hypothesis is strongly committed to the point that sensory attenuation occurs only when the afferent events can be predicted. Only those afferent events specifically attributable to the movements should be attenuated and not all the afferent signals. The studies described above showed that spatio-temporal congruency between the movement and the sensory consequence is a necessary condition for sensory attenuation to occur. According to this model, awareness of our own actions is largely dependent on the outcome of the comparison between the predicted and the actual state of our bodies (but see Fourneret & Jeannerod, 1998).

Given that only self-generated sensory stimulation is attenuated, this effect can also serve as an index of the origin of the afferent signals. In the case of little or no discrepancy between predicted and actual state, one can be reassured that she was the agent. As such, the phenomenon of sensory attenuation may be a functional signature of the bodily self in action, along with the intentional binding (see Section 13.1.1), and can be used as an implicit measure of agency (c.f. Sato & Yasuda, 2005).

1.3.2. Neural Signatures of Agency

An agent performs intentional and voluntary actions. These actions are also experienced as owned. Thus, the neural signatures of agency must reflect the unique neural networks that underpin both the generation of intentional voluntary actions and the experience of self-ownership or self-attribution.

1.3.2.1. Intentional voluntary actions

Agentic behaviour involves the generation, execution, monitoring and perception of voluntary motor actions. Emphasis is given to two aspects of intentional actions that are also constitutive of the phenomenology of agency: the source of the actions (i.e. the intention), and the perception of its effects.

Motives and intentions

The supplementary motor area (SMA) is considered to be the brain structure responsible for translating motivational states originating from anterior cingulate cortex (Paus, 2001) into intentional motor programs. SMA activity precedes M1 activation during the generation of voluntary movement (Cunnington et al., 2002; Deecke et al. 1997; Lee, Chang & Roh, 1999; Weilke et al., 2001), and this activity is present even when a planned movement does not occur (Libet et al., 1983a). According to Deecke, SMA is upstream "in the final motor cascade when it comes to channelling motivation, intention or the act of will into motor execution" (Deecke et al. 1997,p.3). Moreover, its activity seems to reflect a higher-level representation of motor preparation and execution since it is not correlated to the actual muscle activity (Dettmers et al., 1995; Smith, 1979). It has also been documented that magnetic stimulation over SMA can alter the choice of the movement to be executed (Ammon & Gandevia, 1990; see also Brasil-Neto et al., 1992). More direct evidence regarding the role of SMA in translating intentions into actions comes from Fried and colleagues (1991) who studied the functional organization of SMA in 13 patients with intractable epilepsy. Four patients who received direct electrical stimulation in SMA, below the threshold of afterdischarges, reported a subjective "urge" to move or an anticipation that a movement was about to occur. At some of the sites where this "urge to move" was elicited, higher current stimulation produced overt motor behaviour. Overall, these observations argue in favour of Goldberg's view that SMA "[...] functions in a "supramotor" (Orgogozo & Larsen,

1979) fashion, participating earlier than M1 in the translation of motive to intention to action and exerting control over M1" (Goldberg, 1985, p.586).

Selecting an action

Given that a certain goal can be achieved in various ways, the *selection* of the motor program that will be executed is a central problem in the generation of intentional actions. Frith and colleagues (1991) asked subjects to make routine acts as response to stimuli, or to perform open-ended willed actions. Increased activation in the left dorsolateral prefrontal cortex (DLPFC) was found only for the internally-generated responses (i.e. "willed" responses). According to Frith (2000) these results suggest that the role of DLPFC is that of "sculpting the response space" from which the subject can actively choose an action according to his own will.

Planning and perception of self-generated actions

Parietal cortex is a multimodal area, in which both efferent and multimodal afferent signals converge in order to represent accurately the current state of the organism in relation to its environment. Andersen and Bueno (2002) argued for the presence of various "intentional maps" in the posterior parietal cortex (PPC), which correspond to specific goals for orienting actions. The common functional principle of the PPC is to transform multisensory signals into appropriate motor plans or "motor intentions" (Toni, Thoenissen & Zilles, 2001).

Parietal cortex is also involved in the on-line monitoring and perception of actions and their consequences. Fink and colleagues (1999) investigated the neural responses during a conflict between the intention to move and the afferent feedback. In some trials subjects performed out-of-phase bimanual movements, but they saw in-phase movements. The main effect of out-of-phase movements (i.e. a mismatch between intention, proprioception and visual feedback) was associated with increased activity in PPC and DLPFC bilaterally (see also Leube et al., 2003a). It seems therefore that parietal cortex plays a pivotal role in detecting mismatches between the intended and the actual movement, especially in cases where there is ambiguous visual feedback (for a review see Blakemore & Sirigu, 2003). The parietal cortex functions as a neural workspace that facilitates the integration of efferent, re-afferent and ex-afferent signals. Overall, it has

been suggested that the intact function of fronto-parietal neural loops is necessary for the generation, execution and perception of intentional actions.

1.3.2.2. Self-ownership

Several neuroimaging studies have sought the brain bases of self-representation. In Table 1-1, a summary of the main activations reported in 8 neuroimaging studies is presented. In all these experiments, the attribution (of action, memories, verbal processing, 1st person perspective) to self was contrasted to the attribution (of action, memories, verbal processing, 3rd person perspective) to another agent.

Table 1-1 A summary of recent neuroimaging studies on self-processing

Study	**Task**	**Comparison 1st-3rd person**	**Brain Activation**	**Comparison 3rd-1st person**	**Brain Activation**
Ruby & Decety (2001)	Simulation of action	Simulation in 1st person	L Inferior parietal, SI/SII	Simulation in 3rd person	L Cingulate R Inferior Parietal
Farrer & Frith (2002)	Attribution of agency	Self-attribution	Anterior Insula	Other -attribution	R Inferior Parietal
Chaminade & Decety (2002)	Imitate or Imitated	Being imitated	R Inferior parietal	Imitate	L Inferior Parietal
Blakemore et al. (2003)	Delusion of control in hypnotized subjects	Own agency	R SI/SII, Premotor, SMA Insular Cortex, L Cerebellum,	Delusion of control	L Inferior Parietal Insula, Cerebellum bilaterally
Farrer et al. (2003a)	Action-recognition	In control of action	R Posterior Insula	Not in control of action	Inferior Parietal (bilateral)
Fink et al. (1996)	Memory	Personal vs. Impersonal Memories	R Insula R Cingulate Cortex R PFC	Impersonal vs. Personal Memories	*Not reported*
Kirhcer et al (2001)	Face processing	View Own Face vs. Unknown Face	R Insula R. Anterior Cingulate L PFC	Unknown Face vs. Own Face	*Not reported*

Two studies reported activation in the right inferior parietal lobe when subjects simulated an action in 3rd person perspective (Ruby & Decety, 2001), and when they attributed an action to someone else (Farrer & Frith, 2002). Anterior insula was activated

when the action was simulated in 1st person perspective (Ruby & Decety, 2001), and when action was attributed to the self (Farrer & Frith, 2002). Similar activation in the insular cortex was found during self-processing of autobiographical memories (Fink et al., 1996), verbal self-processing and perception of one's own face (Kircher et al., 2000, 2001). In a recent study (Farrer et al., 2003) subjects were presented with various degrees of distorted visual feedback of their own actions and they judged whether the action they saw was their or not. Activity in the right posterior insula was correlated to the match between the performed and viewed movement, and thus with self-attribution. Conversely, activity in the right inferior parietal lobe was associated with dis-attribution of action (see also Blakemore et al., 2003).

Summary

The search for the neural signatures of agency can be summarized in the following three points:

i. Frontal areas, and in particular the supplementary motor area is involved in the early stages of action generation,

ii. Posterior Parietal cortex is involved in the formation of a neural workspace that integrates efferent, re-afferent and ex-afferent signals.

iii. Insular Cortex and Inferior Parietal Lobe were associated to the process of self- or other-attribution of actions, but also in self- and other-processing.

The review on the functional signatures of the bodily self in action showed that both the perceived time of actions and effects, and the perceived intensity of self-generated effects are modulated by the agentic nature of the action. Two functional signatures were identified: intentional binding and sensory attenuation. Both signatures seem to reflect the operation of predictive processes, such as motor intention, efference copy and the forward model. One important difference between the two, lies in their implications for the sense of agency. According to intentional binding, the sense of agency seems to be embedded in the generation of action, whereas according to sensory attenuation, agency is generated through the perception of the effects of the action.

Whereas for both phenomena the presence of efference is necessary, it is not clear whether the efferent signal may also serve as a marker for the ownership of the

action before processing of the sensory feedback. For example, would sensory attenuation occur in situations where the agent performs a self-generated movement whose sensory consequence cannot be predicted by the forward model across all dimensions? This may occur in a case where the sensory effect is predictable across time, but its sensory magnitude may not be. Under normal circumstances, the mere presence of efferent information should constitute an infallible, or at least a necessary index of the source and ownership of action, and it is debatable whether agency attribution needs to rely on sensory feedback. One way to investigate this hypothesis is to create a situation where the efference copy cannot be used by the forward model to predict the magnitude of the sensory outcome. It is an empirical question whether similar sensory attenuation or intentional binding would occur in such conditions. The specific role of efferent information for agency is addressed in the experiments described in Chapter 2.

1.4. Towards a neuroscientific understanding of body-ownership

1.4.1. The Body in the Brain

The representation of the body in the brain cannot be merely reduced to a registration of peripheral inputs. Lesions of the primary somatosensory cortex induce deficits in the tactile and proprioceptive sensations, but there is no evidence that they can cause alterations of higher-order body-awareness (for a review see Berlucchi & Aglioti, 1997). Higher-order disorders of body-awareness, such as anosognosia for hemiplegia (Pia et al., 2004), somatoparaphrenia (Bisiach, Rusconi, & Vallar, 1991), and autotopagnosia (Sirigu, Grafman, & Bressler, 1991) are frequently observed after lesions that involve the parietal lobes (for a review see Haggard & Wolpert, 2005).

Body awareness relies upon a large neural network where somatosensory cortex, posterior parietal lobe and insular cortex play crucial and dissociable roles (Melzack, 1990). It involves the perception of sensory inputs, the interpretation of these inputs in the context of a rich internal model of the body's structure, and the use of these inputs for an on-line representation of the body in space. In fact, recent research on neuropsychological deficits supports the idea that multiple representations contribute to body-knowledge. Sirigu et al. (1991) argued for a distinction between a semantic representation ("body image"), a structural representation ("body structural description"), and an on-line, sensory-motor representation of the body in space ("body schema"). Investigations of patients with brain lesions have provided support for this account. Thus, Buxbaum and Coslett (2001) reported single subjects with selective deficits of the "body structural description" and the body schema (see also Coslett, 1998). In addition, accumulating data demonstrate that the lexical-semantic knowledge of the human body constitutes a relatively discrete semantic domain that may be selectively preserved or disrupted (Coslett et al., 2002; Shelton et al., 1998; Suzuki et al., 1997).

Two key terms in the discussion of how the body is represented in the brain are the "body image" and the "body schema". Usually, the terms of "body image" and "body schema" are used indiscriminately, with ever-changing meanings between authors. The body schema has been interpreted as the knowledge or conscious awareness of the body (Gerstmann, 1927, Klein, 1930, cited in Poeck & Orgass, 1971), as an image (Lhermitte,

1939), as cerebral representation of the body (Hauptmann, 1928, Lange 1936, cited in Poeck & Orgass, 1971), as a preconscious physiological function (Head & Holmes, 1911; for a review see Poeck & Orgass, 1971).

In recent years, the "body schema" has been linked to innate, sub-personal body representations hardwired in the brain, whereas the "body image" usually refers to one's perceptual relationship to one's own body. According to Gallagher (2003), the concept of body image refers to the appearance of the body in the perceptual field. In contrast, the concept of body schema denotes the way the body shapes the perceptual field. Another way by which the body schema can be distinguished from the body image has been proposed by Paillard. In a way that resembles the two visual systems (the "where" and the "what" systems, see Ungerleider & Mishkin, 1982), Paillard (1999b) suggested that the body schema is in fact the "where" system of kinaesthetic information, whereas the body image is the "what" system of perceptual identification of body features. It was then assumed that proprioceptive information is necessary for updating the body schema, whereas exteroceptive multimodal information, mainly visual, underpins the central representation and percept of the body image. Recently, Coslett, (2005) distinguished between the "body concept" and the "body percept". The former was described as "the definition a subject has of his own body whether it is on a conscious or unconscious level" (p. 198); in contrast, the "body percept" was considered to be a representation of the body derived from sensory-motor interactions with the world.

Overall, there seems to be a consensus on the fact that the body image refers to the conscious knowledge and perception of one's own body, while the body schema is an internal model of the body that supports an implicit, subpersonal, knowledge that encodes the body's form, the constraints on how the body's parts can be configured, and the consequences of this configuration on touch, vision and movement. Thus, one way to study this body model is in terms of the way it constrains multisensory interactions. These constrains on multisensory integration are briefly reviewed in the following section.

1.4.2. Examples of Multisensory (Bodily) Interactions

Proprioception derives originally from the local forces acting on muscle spindles, joint receptors and tendon receptors. This raw sensory information is ultimately

combined with knowledge of the body's segmental structure in order to produce a representation of the body's current spatial configuration. One example of this transformation from simple joint information to a more complex body representation is the phantom limb phenomenon, in which an amputated arm or leg continues to be experienced as present by the patient, and occupying its former location in space. This phenomenon is thought to involve continued input to areas of cortex formerly responsible for representing the position of the missing limb (for a review see Ramachandran and Hirstein, 1998). The fact that this input is translated into a detailed limb representation indicates that peripheral information is interpreted with reference to a centrally-maintained model of the body's form that continues to exist even in the absence of the limb that is represented.

Under certain circumstances, the brain will update and even distort the model of the body in order to resolve conflicts of information. An example of this distortion is the Pinocchio Illusion (Lackner, 1988). In this experiment, the subject grasps his nose, with eyes closed. Vibration is then applied to the biceps of the grasping arm. The resulting illusion of the arm extension is accompanied by a feeling that the nose has been elongated, just like Pinocchio's. This vivid experience is thought to arise as a result of the brain's attempt to reconcile the continuous tactile input from the nose to the fingertip with the sensation of the fingertip moving away from the nose caused by the muscle vibration.

Visual inputs can influence proprioception, as demonstrated by the phenomenon of visual capture and prism adaptation. For example, viewing one's hand through a prism results in a temporary distortion of proprioceptive perception such that the hand is felt to lie in the location where it is seen (Welch et al, 1979). Another version of visual capture occurs in patients with phantom limbs: if they see the reflection of their intact arm through a mirror, at the location formerly occupied by the missing limb, then movement of the intact arm induces a perception of identical movements in the phantom limb (Ramachandran and Hirstein, 1998).

A striking example of the substitution of proprioception by vision comes from clinical cases of deafferentation (for a review see Cole & Paillard, 1996). Patient IW suffered from an acute sensory neuropathy in which large fibers below the neck have been damaged due to illness (Cole, 1995). As a result, IW lost the sense of touch and

proprioception below the neck. At the onset of his illness, due to the loss of proprioception, IW could not sit up or stand or move his limbs in any controllable way. In the course of the following two years, he gained enough motor control so that he could move and walk. This happened because IW slowly learned to control his movement by visual guidance of his limbs (see Cole, 1997, Gallagher and Cole, 1995).

The body schema can also coordinate more complex relationships among sensory modalities, including three-way interactions (e.g. among touch, vision, and proprioception). Driver and Spence (1998) found that a brief touch on the hand enhanced the subsequent processing of visual stimuli near the hand, because tactile percepts drew visual attention to the region of space near the hand. This enhanced visual processing was anchored to the hand and moved to different locations in space when the hand was moved, even when the hands were crossed.

Overall, this selective review of multisensory interactions and integrations suggests that the unimodal or multimodal sensory perceptions are neither raw nor immediate. Instead, they seem to be processed and finally constructed with reference to an abstract body representation that guarantees the spatial coherence of the body (see also Haggard, Taylor-Clarke & Kennett, 2003). This integrated body representation unites the different sensory modalities by taking into account their unique relation with regards to the body and the world. The process of weighting and integrating different sensory input into a cognitive body schema is essential for the experience of a unified body (de Vignemont, Tsakiris & Haggard, 2005). But are these multisensory processes sufficient for the link between the body and the self, and the experience of body-ownership?

1.4.3. From Body-representation to Body-ownership

Even though in everyday life the link between the body and its self is taken for granted, the cognitive and neural processes by which the body is experienced as linked to the self are far from being fully understood. Indeed, several features of body representation are interpersonal, and seem to operate interchangeably on one's own body or that of others (see Reed & Farah, 1995; Tessari & Rumiati, 2002). An explicit link between the body and the self is therefore required. The need for a neuroscientific

account of the link between the body and the self is most evident in clinical cases of abnormal body-awareness.

1.4.3.1. A case of body-(dis)ownership

Somatoparaphrenia is a neurological condition, which is usually related to anosognosia for hemiplegia, and occurs after pre-dominantly right hemispheric lesions. Patients with somatoparaphrenia believe that their limbs contralateral to the side of the lesion belong to someone else (Bisiach, Rusconi, & Vallar, 1991; Halligan, Marshall & Wade, 1995; Nightingale, 1982), and the disorder is often accompanied by the inability to feel tactile sensations in the 'non-belonging' part of the body. Bottini and colleagues (2002) reported a case of a patient with somatoparaphrenia who thought that her hand belonged to her niece. In this patient, the tactile imperceptions on her "dis-owned" left hand recovered dramatically when she was instructed to report touches delivered to her niece's hand, rather than to her own hand. Through this verbal instruction, the mismatch between the patient's belief about the ownership of her left hand and her ability to perceive touch on it was momentarily recomposed. This finding suggests that body-ownership involves not only awareness of primary sensory percepts, but also "a crucial contribution from a higher-level representation of the body, including basic beliefs, such as ownership" (Bottini et al. 2002, p.250).

This single case demonstrates the complexity of body-ownership and the intrinsic difficulties encountered in the attempt to understand in neuroscientific terms what exactly is "the body in the brain" (Berlucchi & Aglioti, 1997), but also what is the body for the self.

1.4.3.2. Two phenomenological signatures of the bodily Self

One inherent difficulty in the neuroscience of body-ownership comes from the fact that the body is always present. It would be therefore impossible to design an experiment where the sense of body-ownership could be isolated, by direct manipulations making it present in one experimental condition and absent in another. However, two recent experimental paradigms can be used to investigate the respective contributions of sensory-motor signals and body scheme representations to body-ownership. Both paradigms represent explicit experiences of body-awareness, such as self–recognition and self-attribution of a body-part. Self-recognition refers to the process

of integrating different sources of information (i.e. intentions, efference and motor command, afference) in order to ascribe a visual representation of a body-part to its proper owner (Jeannerod, 2003a). Self-attribution (or incorporation) is the process by which an external object (e.g. a fake hand) becomes part of the bodily self (Tsakiris & Haggard, 2005a). In both paradigms, a body-part is *objectified*, that is, a body-part is presented like an *object*, as a hand projected on a screen, or a fake hand. Then, the empirical question is to investigate the necessary and sufficient conditions under which this body-part will be experienced as infallibly *me*. That is, what patterns of multisensory inputs are responsible for body-ownership?

Self-attribution

In the self-attribution paradigm, subjects are presented with a rubber hand in front of them, while their own hand is out of view. Then, the rubber hand is stroked synchronously with the subject's own unseen hand. The correlated visuo-tactile correlation causes the rubber hand to be attributed to one's own body, to "feel like it's my hand". A behavioural proxy of this attribution process is a drift in the proprioceptively perceived location of the subject's own hand. In one study (Botvinick & Cohen, 1998), after 30 minutes of synchronous stimulation on the rubber hand and the participant's hand, participants perceived their hand to be closer to the rubber hand than it really was. According to Botvinick and Cohen, this Rubber Hand Illusion (RHI) reflects a three-way interaction between vision, touch and proprioception: vision captures touch, resulting in a mislocalisation of the tactile percept towards the spatial location of the visual percept. However, saying that vision captures touch would imply that vision alters the content of the tactile perception. In the case of the RHI, the visual and tactile contents do not differ. Therefore, it may be argued that what vision captures is the proprioception of the hand, because visuo-tactile correlation persuades the subject that the seen hand is the same as the touched hand.

Botvinick and Cohen (1998) suggested that intermodal matching is a sufficient condition for "self-attribution" of the rubber hand to one's own body. Other studies reported that it is possible to induce a sense of ownership by stroking the subject's unseen hand, while they viewed a neutral object (such as a shoe or a table) being synchronously stroked (Armel & Ramachandran, 2003). That would suggest that the RHI is the result of a purely bottom-up mechanism, which associates synchronous visuo-

tactile events. On this view, psychological concepts such as embodiment and selfhood are unnecessary, because purely Bayesian principles of statistical correlation are sufficient to extend the body representation, to include even body parts as implausible as tables. In fact, Armel and Ramachandran (2003) argued that the RHI is resistant to top-down knowledge such as cognitive body representations. In the strong version of this model, any object can become part of *me*. However, the literature on body-representation (see section 1.4.2) suggests that the body is a unique perceptual object, and that body-related percepts are not simply correlated, but they are integrated against a set of background conditions that preserve bodily coherence. On this latter view, intermodal matching may not be sufficient for self-attribution. Cognitive body-representations may also play a critical role for self-attribution.

Self-recognition

In self-recognition experiments, afferent signals such as vision and proprioception need to be integrated with efferent signals in order to generate a coherent self-representation (for a review see Jeannerod, 2003a). This self-representation is accompanied by an explicit form of self-awareness (e.g. "this is *me*").

Developmental psychology has used self-recognition paradigms to explore the onset of explicit self-awareness in infants. Some developmental studies suggest that explicit self-awareness in infants comes between the 14th and 18th month: at this period, infants will be embarrassed when they see in a mirror that there is a rouge spot on their face (Bertenthal & Fisher, 1987). However, from the 4th month, infants start playing in front of mirrors and therefore attending to the visuo-proprioceptive contingencies that accompany self-generated movements. In numerous studies, a visuo-proprioceptive incongruence was introduced, and the results suggested that infants were able to discriminate the temporal incongruence between what they did and what they saw (Bahrick & Watson, 1985), and that they were also sensitive to spatial calibration of their own body movements (Rochat & Morgan, 1995; Rochat, 1998). More recently, it has been shown that infants, as young as 4-months of age, were able to discriminate between self- and other's mirror images (Rochat & Striano, 2002). This evidence demonstrates the presence of a pre-conceptual self-awareness in infants that is bodily in its nature. It is possible that this play with movements, vision and proprioception contributes to the pre-

reflective awareness of the same self who will be embarrassed some months later, during more explicit self-reflecting situations, like the 'rouge task'.

In most recent studies on the self-recognition ability of adults (Daprati et al., 1997; Sirigu et al., 1999; van den Bos & Jeannerod, 2003), participants perform a self-generated movement, while they are looking at (a) their own hand, (b) someone else's hand performing the *same* movement, or (c) someone else's hand performing a *different* movement. Subjects are then asked to make an explicit judgment about the identity of the seen hand. According to Jeannerod (2003a; see also van den Bos & Jeannerod, 2002), one main conclusion of these studies is that 'action cues' are used when distinctive movements are made (e.g. in the different movement condition), and that afferent signals (i.e. vision and proprioception) are used when action cues are ambiguous (e.g. in the same movement condition). In these studies, the movements performed by the subjects were always self-generated, and therefore across conditions, both efferent and afferent information were present. To that extent, these studies did not quantify the specific contribution of efferent information. The paradigm of the RHI suggests that if only afferent information were present or used for self-recognition, then the viewed hand would always be attributed to the self, provided that there were no conflicts between vision and proprioception. Thus, it may be hypothesized that for infallible self-recognition, visuo-proprioceptive congruence may not be sufficient. Efference may play a critical role in structuring the perception of bodily-related multisensory signals.

Summary

The body schema is an internal cognitive and abstract model of the body in the brain. It plays a central role in relating concurrent perceptual inputs, reconstructing missing information, enabling the detection and resolution of multisensory conflicts, and supporting an integrated, consistent, and multimodal representation of the body's configuration (for a review Graziano & Botvinick, 2002, Haggard & Wolpert, 2005).

The review on body-ownership showed that two experimental paradigms, the RHI and the self-recognition experiments, can be used to address the relationship between sensory input, cognitive body-representation and self-attribution. However, this review also revealed two new questions:

1. Is intermodal matching a sufficient condition for bodily self-attribution, and hence for body-ownership?

2. What is the specific role of efference for self-attribution and self-recognition?

These questions are addressed in Chapters 3, 4 and 5.

1.5. A Methodological Approach: The Acting *vs.* the Sensory Self

There is a clear link between body-awareness and self-consciousness. My experience of my body reflects the fact that this particular body responds to my intentional actions, and is the site of my bodily feelings (Merleau-Ponty, 1962). Therefore, from a phenomenological point of view, the sense of agency arising from controlling one's own body movements may be quite different from the feeling of controlling an independent object, such as a machine. The experiments presented in the present thesis deal with the "embodied" variety of agency of controlling one's own body. This sense of agency is what makes us experience ourselves as at once a physical and mental entity. The main issue under investigation is the exact contribution of this sense of *embodied agency* to body-awareness.

One fundamental difference between agency and ownership lies in the main signals used for agency and ownership. Agency is characterized by a strong *efferent* contribution, whereas ownership seems to be characterized by a strong *afferent* component. A second difference lies in the contexts within which agency and ownership can occur. Under normal circumstances, agency is experienced only for voluntary actions. The sense of body-ownership, though, is present during agentic actions, but also during passive or externally-generated sensory experiences. One retains her sense of ownership of her body even in situations where the body is passively or involuntarily moving. This implies that the sense of ownership may give rise to different forms of body-awareness, depending on the presence or not of agency. It seems that agency represents something additional to ownership, but what? To answer this question agency must be subtracted from ownership. In order to approach this issue empirically, a methodological framework is needed to study (i) the sense of body-ownership in the absence of a sense of agency, and (ii) the sense of body-ownership in the presence of agency. To that end, the methodological framework put forward in this thesis distinguished between an 'acting' and a 'sensory' self.

The 'acting' self is the source of an action and also the owner of the consequent bodily sensations. The 'sensory' self is solely the owner of bodily sensations that were not intentionally generated, but on the contrary were passively experienced. This

distinction is principally a methodological one, because the normal experience of one's self in the world does not entail two separate entities, an 'acting' and a 'sensory self'. Nevertheless, this distinction can be of great use for a neuroscientific approach on agency, because it allows for the comparison between purely afferent events and similar afferent events that are voluntarily generated (i.e. efferent-driven).

The difference between the acting and the sensory self can be illustrated in the following example. Imagine two good friends, for example you and *yourself*, going on a ride with your car. *You* are driving, while *yourself* is sitting next to *you*. *You* are the acting self, while *yourself* is the sensory self. The road is empty, everything goes smoothly and you enjoy the ride, discussing about the British weather. Remember, you have identical bodies, you are both sitting in a car, both receiving the same sensory input to your body. While you discuss, *you*, the driver, remember that *you* forgot something, and *you* decide to brake suddenly and make a u-turn to go back home. As *you* brake and turn the wheel, there is a sudden change : both bodies receive similar sensory input, such as equal gravity acceleration, but at the same the bodily experiences of you two are different : *yourself* bangs his body on the door, swearing at *you* for your bad driving manners, while *you* keep on laughing. *Your* body did not experience this change in acceleration as sudden, and perhaps unpleasant, as *yourself*'s body. *You*, the driver, the acting self, anticipated the sensory changes that were about to happen due to *your* action, while *yourself* could only sense the effect of *your* action. This example illustrates some differences between the acting and the sensory self in an extreme situation. One main difference is that the acting self anticipates what the sensory self will experience as an effect of the acting self's action. The present thesis attempts to highlight the phenomenological and functional differences between the 'acting self' and the 'sensory self' under experimental control.

One way to approach these differences is to investigate the specific ways in comparable afferent events are differentially perceived depending on the presence or absence of efference. One example of this manipulation is presented in Figure 1-3.

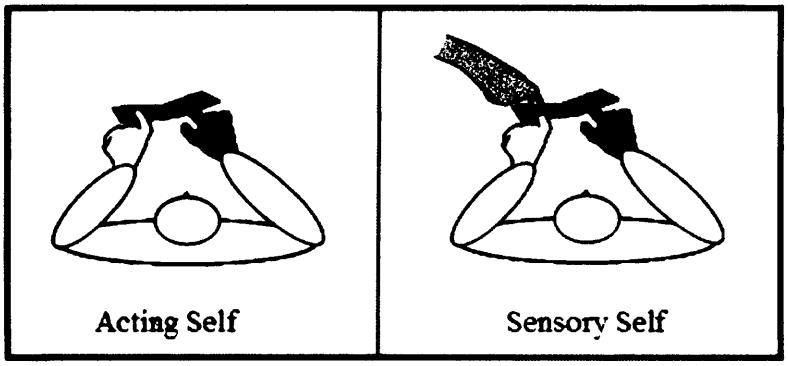

Figure 1-3 An illustrated example of the 'acting' and the 'sensory' self, showing how the methodological distinction between the two can be implemented in an experimental design. The acting self is moving voluntarily his left hand to produce a passive displacement on his right index finger. The sensory self is experiencing a comparable passive displacement on his right index finger, not as an effect of the movement of his left hand, but as an effect of an externally-generated action performed by another agent who pushes the subject's left hand. Thus, efferent information is present only in the first case, whereas it is absent in the second case. Afferent input from the right hand is maintained similar across both cases.

This experimental implementation of this manipulation can investigate (i) how the sense of body-ownership is generated during purely sensory events, and (ii) how the acting self modulates the experience of the sensory self. To that purpose, the perception of afferent events that are self-generated can be compared to the perception of similar afferent events that are either passively or externally-generated. In the present thesis, this comparison will be applied in the domain of action-experience (i.e. time-perception, and sensory-attenuation), and in the domain of explicit body-experience (i.e. self-recognition, and self-attribution).

1.6. Overview of Experiments

The present thesis investigates the ways in which agency and ownership interact across four varieties of self-related experience: time-awareness, somatosensory perception, self-recognition, and self-attribution.

The review of the relevant literature indicated the existence of two functional signatures of agency: intentional binding and sensory-attenuation. One element that seems to be a necessary condition for these phenomena to occur is the presence of efferent information. In Chapter 2, the specific contribution of efference is linked to these functional signatures of the acting self that have been previously identified in the literature: (i) intentional binding, and (ii) sensory attenuation.

With regards to the sense of ownership, the review suggested the presence of two experimental paradigms (i.e. self-recognition and self-attribution) that allow the manipulation of body-ownership. Chapters 3, 4 and 5 focus on these two phenomenological signatures (i.e. self-recognition and self-attribution) of the bodily self. The experiments reported investigate (i) the specific contribution of efferent information to self-recognition in Chapter 3, (ii) the functional, neural and phenomenal correlates of body-ownership by using the paradigm of the Rubber Hand Illusion (RHI) in Chapter 4, and (iii) the body-awareness of the sensory and the acting self during the Rubber Hand Illusion in Chapter 5.

Brief summaries of the experimental questions addressed in the experiments presented in this thesis are provided below.

1.6.1. Time-awareness

Time-awareness refers to the perceived time of actions and their sensory effects (Haggard, 2003). The cognitive neuroscience of time-awareness of action has shown that the perceived times of voluntary operant actions and their effects are temporally attracted towards each other in awareness. This temporal attraction has been termed intentional binding. The specific question addressed in Experiment 2.1 is whether the time perception of voluntary actions and their effects is different from the time-perception of

involuntary movements and comparable effects. That is, what is the influence of agency, and more specifically of efference, on time-awareness of bodily events?

1.6.2. Somatosensory Perception

Sensory attenuation refers to the well-documented phenomenon of attenuating the sensory consequences of self-generated movements. This occurs because in the case of self-generated movements, the internal models of the motor system use the efferent information to produce accurate predictions of the sensory outcome. Moreover, the phenomenon of sensory attenuation has been treated as an index of authorship of action. On this view, self-ascription of actions is not a predictive process based on the presence of the efference copy, but it is the output of a verificational process of comparing the predicted with the actual outcome. The question addressed in Experiment 2.2 is whether such sensory attenuation occurs even when the motor system cannot accurately predict the magnitude of the sensory consequences of self-generated movements: Is the transformation of efferent information into sensory coordinates by the forward model a necessary part of sensory attenuation? In particular, Experiment 2.2 investigates whether a pure efferent signal that need not be processed by the forward model can nevertheless modulate the perception of the intensity of unpredictable somatic effects. If such modulation occurs even under these circumstances, then agency would be a correlate of the generation of efferent information, arising in advance of the sensory feedback.

1.6.3. Self-recognition

Previous studies on self-recognition (Daprati et al., 1997; Sirigu et al., 1999; van den Bos & Jeannerod, 2002) have failed to dissociate between the respective contributions of efferent and afferent information, because the performed movements were self-generated. To that extent participants had both efferent and afferent signals available to inform their self-recognition judgment. In Experiment 3.1, the specific contribution of efference was investigated in an experimental design that selectively manipulated efferent information on the left hand, while afferent information originating from the right hand was held constant. Participants were asked to judge the identity of a visually presented moving hand, which was either their own or someone else's hand, while their own right hand was moving either as an effect of the action of their left hand, or as an effect of an externally-generated action.

1.6.4. Self-attribution

The Rubber Hand Illusion (RHI) provides an experimental paradigm that allows the investigation of the necessary and sufficient conditions for bodily self-attribution, and thus body-ownership. The experiments focus on (a) the influence of general body scheme representations on the RHI (Experiments 4.1 & 4.2), (b) the neural correlates of body-ownership (Experiment 4.3), (c) the necessary conditions of visuo-tactile stimulation underlying the RHI and its effect on body-awareness (Experiments 5.1 & 5.2), and (d) the role of agency for self-attribution and body-awareness during the RHI (Experiment 5.3).

2. Experimenting with the Acting Self[1]

2.1. Introduction

In the case of a self-generated action, intentions and efference copy should predict the consequent visual, auditory and somatosensory signals produced by our movements. Intentions and motor commands can thus be used to distinguish the sensory consequences of our own actions from externally produced sensory stimuli (for a review see Blakemore & Sirigu, 2003). As a consequence, we can refer an action to its proper agent and effectively distinguish the self from others (Blakemore, Wolpert & Frith, 2002, but see de Vignemont & Fourneret, 2004; Georgieff & Jeannerod, 1998). It has been postulated that a central monitoring system (Frith 1992) or an internal 'forward model' (Wolpert 1997) compares the predicted sensory outcome of our own actions with the actual somatosensory feedback. The cerebellum is thought to be involved in signalling the sensory discrepancy or similarity between the predicted and the actual sensory consequences of our movements (Blakemore, Frith & Wolpert, 2001).

In accordance with this view, somatosensory consequences of our own actions are perceived differently from identical somatosensory inputs that are externally generated. Numerous studies have shown that the perceptual consequences of self-generated actions are attenuated compared to similar sensory effects that are externally-generated (Blakemore, Frith & Wolpert, 1999; Blakemore, Wolpert & Frith, 1998, 1999; Claxton, 1975; Collins, Cameron, Gillard & Prochazka, 1998; Weiskrantz, Elliot & Darlington, 1971; for a review see Blakemore, Wolpert & Frith, 2000). Blakemore and colleagues (1998, 1999, 2000) have argued that the ability to *predict* and *anticipate* the consequences of our own actions underlies this differential perception of identical somatosensory stimuli when they are self-generated compared to when they are externally generated.

In a similar way, a series of experiments has shown that the time-awareness of actions is *anticipatory*: we perceive our actions to occur slightly earlier that they really do (Haggard & Eimer, 1999; Haggard & Magno, 1999; Haggard et al., 2002; Libet et al., 1983). One explanation put forward is that the perceived time of action is modulated by

[1] Experiments 2.1 and 2.2 were published in Tsakiris M & Haggard P (2003). Awareness of somatic events associated with a voluntary action. *Experimental Brain Research* **149**, 439-446.

processes of intentional and motor preparation that precede the action itself, in a way similar to the operation of the forward model during sensory prediction and anticipation. It has been shown that the perceived time of sensory effects caused by an action may also be influenced by the intentional nature of the causative action: when an action caused an auditory tone, then the time-awareness of the action and the auditory tone showed an attraction in time towards each other (Haggard et al., 2000; Haggard, Clark & Kalogeras, 2002). This temporal attraction has been termed "intentional binding" (Haggard, Clark & Kalogeras, 2002). This effect was found to be specific to operant voluntary actions, that is, actions that do cause an effect, and did not occur when the auditory tone occurred after an involuntary movement (Haggard, Clark & Kalogeras, 2002), or when two tones occurred, or when a tone was followed by a reactive movement (Haggard et al., 2002).

Both the sensory attenuation and the intentional binding phenomena seem to be present only for agentic movements (but see Chapman et al., 1987; Collins et al., 1998), yet they seem to modulate the perception and awareness of one's own body (i.e. the sense of body-ownership). Both phenomena underlie agency, and they seem to arise from pre-action and action-related processes. In particular, they are both linked to the predictive and anticipatory function of the motor system. Given that self-generated movements presuppose the presence of an efference copy, efferent information may play a critical role in the generation of these two functional signatures of the acting self.

The experiments presented in this chapter aimed at investigating the way the brain uses efferent information to link actions and their subsequent somatic effects in time- and sensory-awareness. Given that efference is present only in voluntary movements, it is hypothesized that its presence may also be sufficient for the experience of agency. According to the "forward model of agency" (see Section 1.2.4.2), ascription of agency is not possible until the comparison between the predicted and actual sensory feedback. Thus, on that view, efference does not carry any intrinsic information regarding the source of the action that could actually be used as the basis of the sense of agency. The neuroscience of time-awareness of action has shown that at least initial awareness of action is based on pre-action processes, and therefore the efference copy may support an initial sense of agency. One way to test whether efference can provide a sense of agency is to examine the effect of efferent information on the two functional

signatures of the acting self that were previously described, namely, the intentional binding and the sensory attenuation. If efference was sufficient to produce these two effects, then one could argue that efference drives our sense of agency.

Experiments 2.1 and 2.2 tested this hypothesis by comparing awareness of somatic effects caused by a voluntary action to awareness of similar somatic effects following a passive involuntary movement that was physically similar to the voluntary action. Importantly, the predictive information that efference carried was minimized to ensure that it could not be used by the forward model to predict the magnitude of the consequent somatic effect (see also Shergill et al., 2003). The minimal efferent information could provide only a raw temporal signal related to the onset of the action, and it could possibly predict only the onset of the imminent somatic effect. This "raw" efferent signal cannot be directly compared to the re-afferent feedback, since the former is a copy of a motor command, whereas the latter is a sensory signal. It was hypothesized that this "raw" efferent signal may serve as a pragmatic index of agency of action, and as such it may underlie the inducement of intentional binding and sensory attenuation.

2.2. Experiment 2.1: Efference and Intentional Binding

> *"It is indeed true that I should be incapable of perceiving any point in time without a before and an after, and that, in order to be aware of the relationship between the three terms, I must not be absorbed into any of them: that time, in short, needs a synthesis [...]Time is therefore, not a real process, not an actual succession that I am content to record. It arises from my relation to things"*
>
> *Merleau-Ponty (1962, 415)*

2.2.1. Introduction

In the present experiment, the aim was to generalise the 'intentional binding' mechanism to somatic effects by addressing the specific role of agentic voluntary movements. Any action involves two distinct elements: a motor command, and consequent body movements or somatic effects. The term somatic effect is used to refer to physical stimulation of the body that arises as a direct consequence of the motor command. Somatic effects may be complex, extended in time, and involve body parts that are not actively controlled. For example, if I use my left hand to push my right arm, the right arm moves as a somatic effect of the left hand's action. The brain's predictive attribution process should link the movement of the right arm to the voluntary action of the left hand, and not consider it as a separate action. Because somatic effects always accompany action, they offer a more ecological test of the "intentional binding" mechanism than arbitrary auditory effects of action studied previously (Haggard, Clark and Kalogeras, 2002).

In particular, the present study investigated whether the time-awareness of actions and subsequent somatic effects is modulated by agency. Thus, the time-awareness of somatic effects caused by a voluntary action was compared to the time-awareness of similar somatic effects caused by a passive involuntary movement. To investigate whether the brain links representations of actions and somatic effects, these events were deliberately separated in time, and were localised to different body parts. A voluntary or involuntary movement of the left index finger caused a somatic effect, a twitch evoked by TMS, on the right index finger. The use of TMS ensured that the somatic effects were constant across conditions (see section 2.2.2). The parameters of movement of the left hand were identical (a key press) across voluntary and involuntary conditions. What differed in these two conditions was the voluntary or involuntary origin

of the key-press event. Moreover, the causal relationship between the key press and the somatic effect was held constant across conditions. Only the authorship of the action (i.e. agency) was different and systematically manipulated across conditions. Thus, the sense of agency was manipulated on the left hand, whereas the sense of ownership was maintained constant on the right hand for both the voluntary and involuntary contexts.

Based on previous experiments (Haggard et al., 2002; Haggard, Clark & Kalogeras, 2002), the hypothesis predicted the presence of a significant temporal attraction between the voluntary movement and the subsequent somatic effect. Efferent information would be necessary for this binding effect. Thus, when the movement that triggered the somatic effect was involuntary, the hypothesis predicted the presence of a temporal repulsion between the involuntary movement and the somatic effect.

2.2.2. Experimental Design, Methods and Participants

Experimental Design

The experiment consisted of three baseline and four operant conditions (see Table 2-1). Across all conditions, the participants' task was to judge the time-onset of a given event in each trial.

Table 2-1 Baseline and Operant Conditions of Experiment 2.1

Condition	Event Judged	Event Position	Context
Single-event baseline conditions			
1 Voluntary Key-press	Voluntary Key-press	1	Baseline
2 Involuntary Key-press	Involuntary Key-press	1	Baseline
3 Somatic Effect	Somatic Effect	1	Baseline
Operant conditions			
4 Voluntary Key-press, causing a Somatic Effect	Voluntary Key-press	1	Voluntary
5 Voluntary Key-press, causing a Somatic Effect	Somatic Effect	2	Voluntary
6 Involuntary Key-press, causing a Somatic Effect	Involuntary Key-press	1	Involuntary
7 Involuntary Key-press, causing a Somatic Effect	Somatic Effect	2	Involuntary

In the single-event baseline conditions, only one event occurred per trial. In the first baseline condition, subjects were instructed to press a key voluntarily at a time of their own free choice with their left index finger, and judge the onset of their voluntary action. In the second baseline condition, subjects were instructed that the key press would be generated passively by a mechanical displacement applied by a computer-controlled motor to the subject's left index fingernail. Again, subjects were asked to judge the onset of the involuntary key-press. In the third baseline condition, TMS over the optimal location in the left motor cortex for exciting the first dorsal interosseus (1DI) of the right hand was applied under computer control, and subjects were instructed to

judge the onset of the twitch of the right index finger. The TMS-twitch was used in this study to produce a somatic effect whose time-onset could be accurately measured, and whose objective intensity could be accurately quantified. These baseline conditions served to establish the perceived time of each event when it occurred alone. This is required to control for individual differences in time estimation and in the division of attention between the clock and the judged events (see section 2.2.4).

In each of the four operant conditions, two events occurred per trial, a movement of the left index finger (voluntary or involuntary key-press) and a somatic effect experienced on the subject's right index finger. These two events (i.e. the key-press and the somatic effect) were causally linked across conditions. The response key positioned by the left hand was connected to a TMS placed over the left motor cortex. Participants were informed that the key could be pressed either voluntarily or passively by the index finger of their left hand, causing a TMS-induced twitch of their right index finger. The time interval between the action and the effect was set at 270ms in all operant conditions (see Figure 2-1).

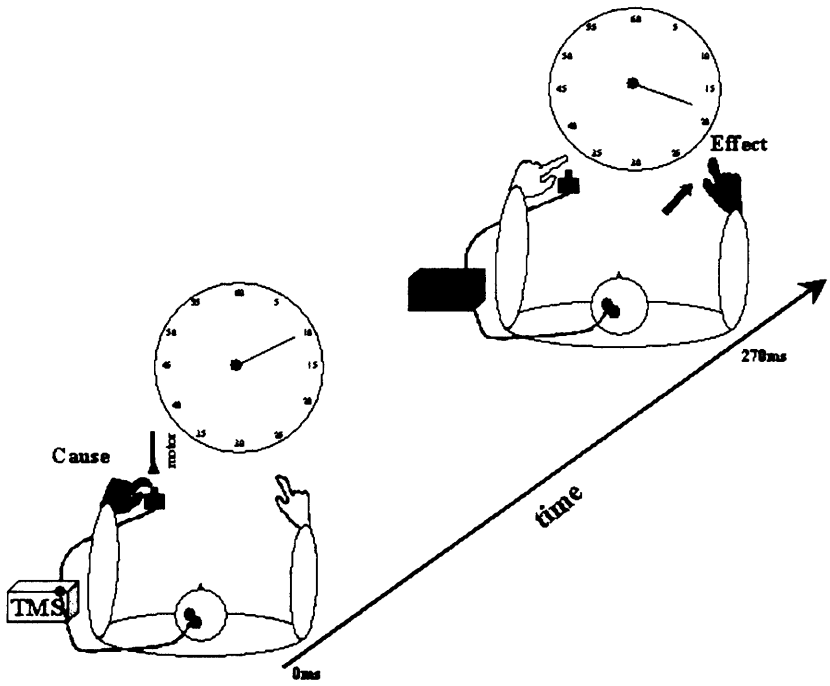

Figure 2-1 The experimental set-up in the operant conditions in Experiment 2.1. A key press triggered the TMS which was applied over the motor cortex of the participant, producing a twitch of the right index finger 270ms later. The key was pressed either voluntarily by the participant's left index finger or

by an involuntary movement (e.g. the motor was pressing the participant's finger on to the key). Participants had to judge the time onset of any of these events in different conditions.

Thus, in the operant conditions the key-press was defined as the causative action, and the TMS-induced twitch was the somatic effect of this action. Here, TMS was used to induce a somatic sensation on the right hand, as a consequence of a voluntary or involuntary movement of the subject's left hand. It has been recently shown that the sensation of movement elicited by TMS is due to sensory feedback, and not due to an efferent signal (Ellaway et al., 2004; see also Chronicle & Glover, 2003). Thus the somatic sensation produced by the TMS was purely afferent in nature.

The four operant conditions were arranged as a 2x2 factorial design. The factors were the event judged by the subject (the movement of the left index finger or the somatic effect), and the type of "movement" that produced the somatic effect (voluntary vs. involuntary movement).

Methods

Participants were instructed not to press the button in a stereotyped way, to avoid acting at a fixed latency after the start of the trial, to avoid choosing to act at pre-decided positions of the clock hand, and to ensure that the clock rotated at least once prior to their action. Before the experiment, participants performed training blocks (10 trials per block) for the three baseline conditions. During the main experiment, each condition was performed in a separate block. Each participant performed the blocks in a different random order. Each block contained 31 trials, and the first trial of each block was not included in the analysis. A small number of trials (4%) had to be discarded due to technical failures or participants' failure to follow instructions.

Participants judged the perceived time of sensory and motor events, using a method developed by Libet et al. (1983b). Participants viewed a clock hand (length 12mm) rotating with a period of 2560 ms on a computer screen. The clock face was marked with conventional intervals (5, 10, 15, etc.). The initial clock position was random. Clock rotation was initiated by the experimenter at the beginning of each trial. Subjects reported their judgment at the end of each trial, after the clock hand stopped rotating. Participants judged the perceived time of onset of any of 3 events according to condition, in 7 separate blocks (se Table 2-1).

TMS was delivered using a figure-of-8 coil with a Magstim 200 stimulator (Whitland, UK). The optimal location for producing twitches (MEPs) in the right first dorsal interosseus (1DI) was located by systematically exploring a 1-cm grid over the hand area of the left motor cortex. The motor threshold (MT) was calculated for each subject by reducing stimulator output in 5% steps to find the lowest level at which 3 MEPs exceeding 50μV peak amplitude were obtained from 5 successive stimulations of the relaxed 1DI muscle. Thresholds ranged from 30% to 50% of stimulator output (mean, 40%). Three different TMS output levels were used throughout the experiment: 110%, 130% and 150% of relaxed motor threshold. 10 trials at each output level were used in each block. The level was changed every 5 trials, using a different random order of levels for each block and each subject. EMG was measured from 1DI muscle of the right hand with bipolar recording from surface Ag/AgCl electrodes, amplified and digitized at 5 kHz.

Participants

Twelve healthy naïve volunteers with normal or corrected to normal vision (mean ages 24.3, 5 female, 10 right-handed). Procedures were approved by the institutional ethics committee and participants gave written informed consent to participate in this study.

2.2.3. Results

To recap, the conditions differed according to the context within which the events occurred (single-event baseline or operant), and according to the event judged (voluntary key-press, passive involuntary key-press or somatic effect). Judgement errors were defined as the difference between the actual time of occurrence of the judged event and the perceived time of its occurrence. The judgment errors were calculated for each trial and averaged. A negative judgment error was used for anticipatory awareness of events (i.e. the participant perceived the event happening before it really did), and a positive judgment error was used for delayed awareness (i.e. the participant perceived the event happening after it really did).The mean judgment errors and the mean perceptual shifts from the 12 participants in each condition are shown in Table 2-2.

Table 2-2 Judgement Errors and Mean Perceptual Shifts across conditions.

	Judged Event	**Mean Judgment Error in ms (± *s.d.*)**	**Mean Shift in ms (± *s.d.*)**
Baseline conditions			
Voluntary Key-Press	Voluntary Key-Press	**-10** (± *34*)	
Involuntary Key-Press	Involuntary Key-Press	**-4** (± *90*)	
TMS-induced movement	Somatic Effect	**-17** (± *81*)	
Operant conditions			
Voluntary Key-Press, then TMS-induced movement	Voluntary Key-Press	**16** (± *36*)	**26** (±*37*)
Voluntary Key-Press, then *TMS-induced movement*	Somatic Effect	**-26** (± *86*)	**-9** (±*54*)
Involuntary Key-Press, then TMS-induced movement	Involuntary Key-Press	**-13** (± *60*)	**-9** (±*62*)
Involuntary Key-Press, then *TMS-induced movement*	Somatic Effect	**-2** (± *79*)	**15** (±*69*)

Judgment errors for the three single-event conditions indicated an anticipatory awareness for voluntary key-press (-10ms), a roughly accurate awareness of passive involuntary key-press (-4ms) and an anticipatory awareness for a TMS-induced twitch (-17ms). The mean estimates for the single-event baseline conditions are comparable with previous reports. (c.f. Libet et al.1983b; Haggard et al., 2002 ; Haggard, Clark & Kalogeras, 2002).

To control for factors such as the sensory transmission and division of attention of each participant, and differences in the salience or perceptual centre of judged events, it was necessary to calculate the change in the perceived time of each judged event in the operant context compared to the single-event baseline condition. Thus, the perceived time of each event (voluntary key-press, involuntary key-press, or somatic effect) in the single-event condition was subtracted from the perceived time of the same event in the operant conditions. The term "perceptual shifts" refers to the resulting quantities (see Table 2-2). Perceptual shifts represent the effect of operant context on the perceived time of each event. Positive perceptual shifts indicate that an event is perceived later in the operant context than in the baseline condition, and negative perceptual shifts indicate that an event is perceived earlier in an operant context than in the baseline condition. The calculation of the perceptual shifts effectively controls for the prior entry phenomenon (Sternberg and Knoll, 1973) and for the dynamic allocation of attention, as shown in more detail in the Section 2.2.4.

Perceptual shifts between single-event and operant conditions indicated strong perceptual attraction effects between voluntary actions and their somatic effects, and strong perceptual repulsion effects for involuntary actions and their somatic effects. A voluntary key-press was perceived to occur 26 ms later when it produced a somatic effect than when it produced no effect. Conversely, somatic effects produced by a voluntary key-press were perceived 9 ms earlier than somatic effects generated by computer without any preceding action. That is, voluntary actions were shifted towards their somatic effects, and somatic effects were shifted towards the actions that caused them. This pattern was reversed for passive involuntary movements. A passive involuntary key-press was perceived to occur 9 ms earlier when it produced a somatic effect than when it had no effects. Somatic effects caused by an involuntary key-press

were perceived to occur 15 ms later than the same effects without any preceding event. (see Figure 2-2).

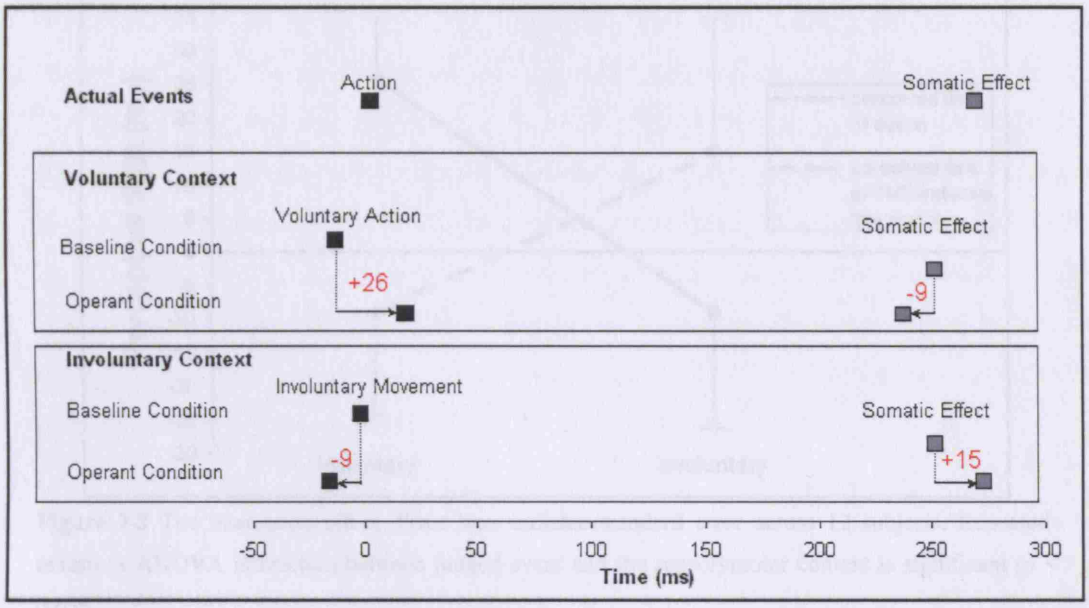

Figure 2-2 A schematic representation of the mean of perceptual shifts (in red).

The mean perceptual shifts were subjected to 2x2 Repeated Measures ANOVA, using two within-subject factors. These were the operant context (voluntary vs. involuntary) and the type of event judged (key-press vs. somatic effect). This analysis showed no significant effect of the operant context ($F(1,11)=0.242$, $p>0.05$), no significant effect of the event judged ($F(1,11)=0.072$, $p>0.05$), but a significant interaction between the two factors ($F(1,11)=7.226$, $p<0.03$). This interaction arose because the voluntary context produced significant temporal attraction effects between voluntary action and its somatic effect, whereas the involuntary context produced repulsion effects between involuntary movement and the same somatic consequence. This pattern of results produces the cross-over interaction seen in Figure 2-3.

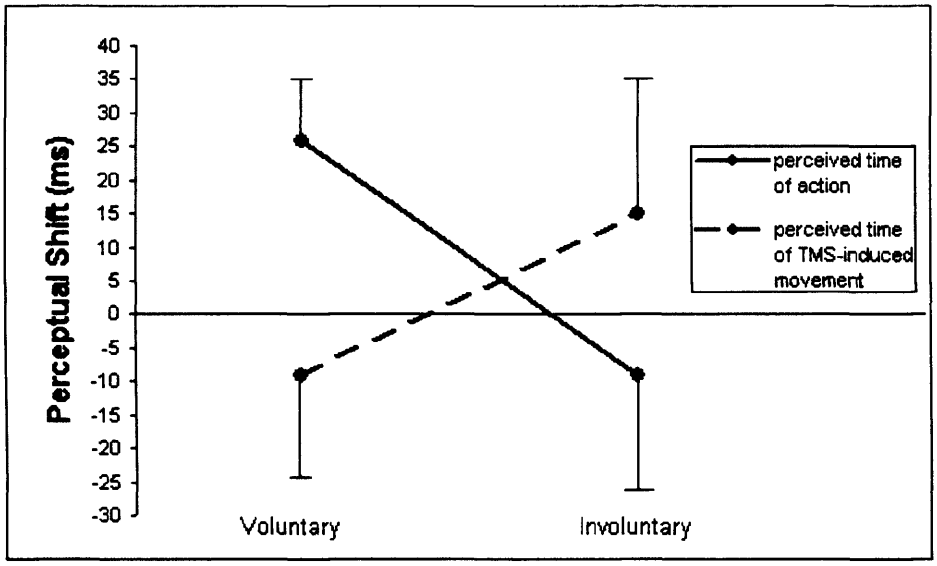

Figure 2-3 The interaction effect. Error bars indicate standard error across 12 subjects. Repeated-measures ANOVA interaction between judged event and the sensorymotor context is significant ($p < 0.03$).

2.2.3.1 Control Analyses

Two further control analyses were performed to investigate possible confounding factors, such as differences in the magnitude of the somatic effect or an unspecific effect of TMS that could have influenced the perceptual judgments.

Physical Differences in MEP size

To investigate whether the differences between voluntary and involuntary context was due to possible physical differences in the MEP size of the somatic effect, a 2x2 Repeated Measure ANOVA was performed on the mean MEP size across conditions. The two factors were the operant context (voluntary vs. involuntary) and the second factor was the event judged (key-press or effect). None of the main effects was significant ($F(1,11)=1.49$, $p>0.05$ for the main effect of context, $F(1,11)=1.05$, $p>0.05$ for the main effect of event judged). Similarly, the interaction of the two factors was not significant either ($F(1,11)=.004$, $p>0.05$). Therefore, the MEP sizes were not significantly different between conditions.

Unspecific effect of TMS

Finally, to investigate whether the observed temporal attraction effect depended on the salience of the somatic effect, a further 3-way ANOVA was performed on the perceptual shifts shown in Table 2-3. The first factor was the operant context (voluntary vs. involuntary). The second factor was the event judged (key-press vs. somatic effect). The third factor was the TMS output level (110%, 130%, and 150% above MT). No significant main effects were observed. The only significant effect involving TMS output level was an interaction between TMS output and event judged ($F(2,22)=7.666$, $p<0.02$). TMS output level had a greater influence on awareness of the somatic effect than on the key-press, which is unsurprising. Specifically, increasing the TMS output level tended to delay the percept of the somatic effect. Importantly, this effect did not interact with the operant context of the key-press ($F(2,22)=0.597$, $p>0.05$).

Table 2-3 Mean perceptual shifts across conditions for the different TMS-outputs

Operant Conditions	**Event Judged**	**TMS=110% of MT**	**TMS=130% of MT**	**TMS=150% of MT**
Voluntary key-press, then TMS-induced twitch	Voluntary key-press	26	22	26
	Somatic Effect	-34	-1	-1
Involuntary key-press, then TMS-induced twitch	Involuntary key-press	3	-10	-14
	Somatic Effect	4	15	41

Overall, the results show that operant voluntary actions elicit a perceptual attraction between the time-awareness of the actions and its somatic consequence. This effect binds together awareness of the voluntary action with awareness of its somatic effect, bringing them closer in perceived time. An involuntary movement produced a perceptual repulsion in the opposite direction.

2.2.4. Discussion

The present study aimed at: (a) generalizing the intentional binding for somatic effects caused by voluntary actions, and (b) investigating whether the perceived time of movements and somatic effects is modulated by agency. The results confirmed the hypothesis that the intentional binding mechanism operates also for somatosensory effects, and not only for auditory tones (Haggard, Clark & Kalogeras, 2002). Moreover, this mechanism is present only when the somatic effects are produced by an agentic movement. First, possible artefactual explanations of the results are discussed.

Previous studies of temporal awareness of action (Libet et al., 1983) have been criticised (Breitmeyer, 1985) because of the prior entry phenomenon (Sternberg and Knoll, 1973). In prior entry, an event on an attended perceptual stream seems to occur earlier than a synchronous event on an unattended stream. The participants presumably divided attention between the clock and the events they judged. Therefore, any single estimate of judgement error depends on the precise division of attention, which is unknown. However, the design of the present experiment involves differences in judgement error between baseline and operant conditions, and it requires only comparable division of attention in both conditions. Moreover, allocation of attention should be comparable for the first event of an operant context and for the same event in a single event, control condition (see also Haggard, Clark and Kalogeras, 2002). The use of perceptual shifts can effectively control for these confounds because they represent the effect of operant context (voluntary vs. involuntary) on the perceived time of each event.

Second, could the presence of the first event (voluntary action or passive movement) cause dynamic reallocation of attention to the somatic effect, producing a difference in prior entry bias between baseline and operant conditions? This suggestion cannot explain why perceptual shifts operate in opposite directions for voluntary actions and for involuntary passive movements. Third, physical differences in movement or the somatic effect cannot account for the different pattern of results across conditions. MEP sizes were not significantly different between conditions. The key press was under identical computer control across all the involuntary conditions, and appeared similar (though not quantitatively measured) across all the voluntary conditions. Thus, the

absence of reliable physical differences between the parameters of movement in single-event and operant conditions and in the actual intensity of the somatic effect suggests that physical differences cannot convincingly explain the pattern of perceptual shifts reported. Fourth, a non-specific effect of TMS on timing judgement cannot account for the opposite pattern of results in the voluntary vs. involuntary conditions. Thus, simple artefactual explanations cannot account for the crossover pattern of perceptual shifts shown in Figure 2-3.

Instead, the results showed that only voluntary actions elicit a temporal attraction between the action and the subsequent somatic effect. When an intentional voluntary action was performed, awareness of the action was bound with awareness of its bodily consequences, bringing the two events closer in perceived time. A passive involuntary movement produced a perceptual repulsion in the opposite direction. Importantly, the parameters of movement in the present study were identical across conditions, and the spatiotemporal relation between the key press and the TMS pulse was also identical. Moreover, the pairing of the key-press with the somatic effects was held constant across all operant conditions. Only the authorship of the action was different across conditions because the sense of agency was manipulated by design: the key-press could be performed either voluntarily or involuntarily. By contrast, the sense of ownership (e.g., the TMS-induced somatic effect) was maintained constant across conditions. The results suggest that the sense of our body is modulated by the voluntary context of a prior action. In particular, "sense of agency," is necessary for this temporal attraction effect to appear, while "sense of ownership" is not sufficient.

The present results are consistent with previous studies on time-awareness of action. It has been suggested that (1) awareness of action depends on central signals, which precede actual bodily movement (Haggard & Eimer, 1999; Libet et al., 1983)), and (2) the volitional character of the movement modulates not only the perception of the action, but also the perception of the sensory stimulus following that action (Haggard et al., 2002; Haggard, Clark & Kalogeras, 2002). Briefly, voluntary actions that produced an external effect were perceived to occur later than voluntary actions that produced no effect. Conversely, external events produced by one's own voluntary action were perceived to occur earlier than comparable events that occurred without agency. Thus, awareness of actions and effects show an attraction in time towards each other, termed

"intentional binding" (Haggard, Clark & Kalogeras, 2002; Haggard, 2005a; Tsakiris & Haggard, 2003). The present study adds several facts to our knowledge of this process. First, the binding process works with a different and more ecological modality of effect (i.e. somatomotor) than previous studies. Second, it does not work with involuntary movements and their identical somatic effects, suggesting that efference is a necessary condition. The binding mechanism is engaged by agency, but not by mere body movement, suggesting that the 'intentional binding' mechanism cannot be dissociated from agency.

2.3. Experiment 2.2: Efference and Sensory-Suppression

2.3.1. Introduction

The predictive operation of the motor system and the process of separating and distinguishing re-afference from ex-afference have been linked to the sense of selfhood and agency (Blakemore Frith & Wolpert, 2002). Sensory attenuation can be conceptualised as an index of authorship: if there is no discrepancy at the level of the comparison between the predicted and the estimated actual sensory feedback, then the origins of the sensation can be traced back to the self (see Figure 2-4). It follows, that the internal forward model of the motor system can support a critical decision as to who caused the effect of an action: if the effect was not attenuated, then the effect was self-generated. Sensory magnitudes are therefore a good candidate dependent variable for studies of agency, because sensory attenuation occurs only when a sensory event can be unambiguously attributed to the self.

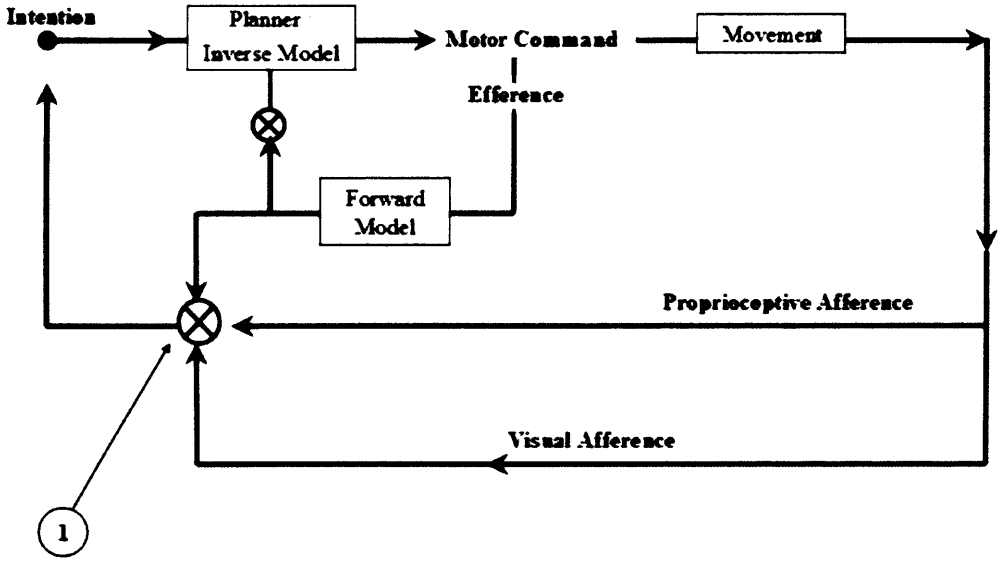

Figure 2-4 The "forward model" of authorship. Intention refers to the desired state of the system's motor behavior. When the motor command is generated, an efference copy of this command is generated in parallel. The sensory consequences of self-generated actions are attenuated because the forward model of the motor system can use the efference copy so as to predict them. When there is no discrepancy between the predicted and the actual feedback, the origin of the sensation or event (which may be a movement) can be attributed to the self (point 1) in the graph.

In relation to the sense of agency, this model implicitly implies that self-ascription of actions is not possible until the perception of the actual afferent signals, and their comparison to the predicted state of the system. However, it could be argued that under normal circumstances, the mere presence of efference copy should constitute an infallible, or at least a necessary, pragmatic index of the source of action, and it is debatable whether self-ascription of an action requires a post-action judgment. On that view, efference would be a sufficient index of authorship of action, to the extent that, by definition, it is present only when an action is *self*-generated. Therefore, it is an empirical question whether efferent information *per se* would be sufficient for the attenuation of self-generated somatic effects, or whether sensory attenuation occurs only when the forward model can transform the efference copy into sensory coordinates that accurately predict the sensory feedback (Shergill et al., 2003; Merfeld, 2001).

One way to investigate this hypothesis is to create a situation where the efference copy cannot directly predict the magnitude of the sensory outcome, and thus it cannot be transformed by the forward model into accurate sensory coordinates used for comparison. According to the "efferent-driven hypothesis" of agency, efferent information may be a pragmatic index of authorship of action, because efference is present only when an action is self-generated. One way to test whether efference generates a sense of agency is to examine the relationship between efferent information and sensory attenuation. If efference is sufficient for producing sensory attenuation without being processed by the forward model, then it could be argued that efference drives our sense of agency. This is schematically demonstrated in Figure 2-5.

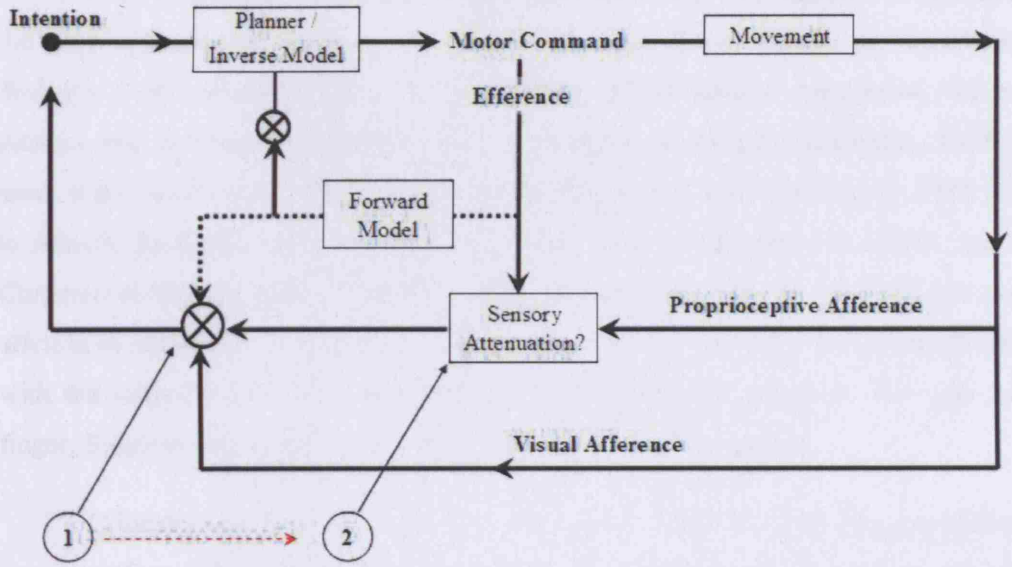

Figure 2-5 In the present experiment, efferent information carries only a temporal signal, and it is not processed through the forward model (dotted lines). The question addressed in the present experiment, is whether efference would be sufficient to induce sensory attenuation (point 2), without the predictions generated by the forward model (point 1).

As in Experiment 2.1., a voluntary or an involuntary key-press produced an unpredictable somatic effect. As in Experiment 2.1, the efference, present in the voluntary condition only, carried minimal predictive information related to the impending somatic effect.

No previous studies have compared the sensory perception of somatic effects that were either self-generated or passively-generated by the *same* person. Previous designs have focused on the perception of somatic effects that were either self-generated or externally-generated, without investigating whether a prior passive movement would produce sensory attenuation (c.f. Blakemore, Frith & Wolpert, 1999). To that purpose, the present design compared the perceived intensity of self-generated somatic effects to the perceived intensity of similar somatic effects that were passively generated by the same person. To do this, the action was dissociated from its effect, because these events were deliberately separated in time, and was localised to different body parts. This manipulation can test the hypothesis that sensory attenuation is not an artefact of the presence of a prior movement *per se*.

Few studies on sensory attenuation have quantified the objective magnitude of the sensory input (but see Bays, Wolpert & Flanagan, 2005; Blakemore, Goodbody & Wolpert, 1998; Shergill et al., 2003). Because in the present experiment, the main interest was to compare objective with subjectively perceived magnitudes, TMS was used. It has been recently shown that the sensation of movement elicited by TMS is due to sensory feedback, and not due to an efferent signal (Ellaway et al., 2004; see also Chronicle & Glover, 2003). Thus the somatic sensation produced by the TMS was purely afferent in nature. As in experiment 2.1, a voluntary or involuntary key-press performed with the subject's left index finger caused a TMS-induced twitch on the right index finger. Subjects were asked to judge the intensity of the TMS-twitch.

Critically, as in Experiment 2.1, the use of TMS allowed the generation of somatic effects whose magnitude could not be predicted by the forward model of the motor system. The TMS output used in each trial was under the experimenter's control (see section 2.2.2). Each key-press, be it voluntary or involuntary, generated an unpredictable TMS-twitch. The delay between the key-press and the occurrence of the somatic effect was set at 270ms across conditions. Therefore, the two conditions differed according to whether the key-press was voluntary or not. The physical parameters of the key-press were identical across conditions. Efferent information was present only in the voluntary conditions, and carried only a raw temporal signal related to the onset of the action. The hypothesis tested in this experiment was whether the presence of an efferent signal would be sufficient for the sense of agency as measured by somatosensory attenuation.

2.3.2. Methods

Using the same logic as in Experiment 2.1, a key press triggered the activation of TMS, which was applied over the motor cortex of the participant, producing a twitch of the right index finger 270ms later (see Figure 2-6). The key was pressed either voluntarily by the participant's left index finger (voluntary condition) or by a mechanical motor pressing the participant's finger on to the key (involuntary condition), or by the experimenter (control condition). No prior movement of the left hand occurred in the control condition.

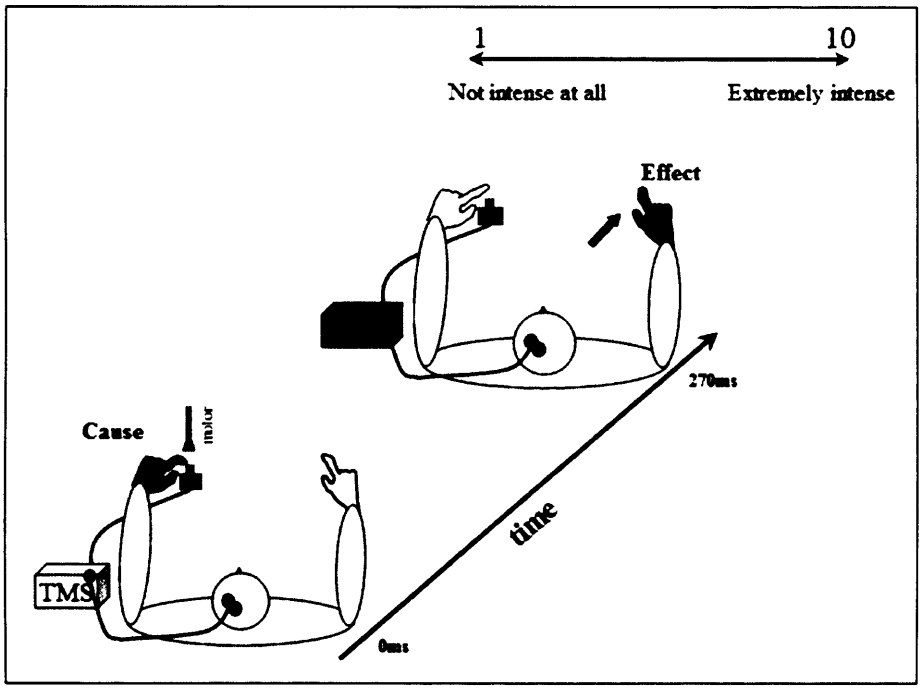

Figure 2-6 Experimental set-up in Experiment 2-2.

Participants were instructed to judge the intensity of TMS-induced twitch of their right index finger by using a subjective scale from 1 to 10, 1 being not intense at all, 10 being extremely intense. The participant's right hand was hidden inside a frame to minimise any possible confounding influence of the view of the twitch on their intensity judgments. Participants were told that the TMS-induced twitches would be similar to intensity to the ones experienced in Experiment 2-1, so as to provide an anchor. To achieve a wide range of actual twitch intensities, the TMS output was varied randomly across trials between 110%, 130%, and 150% of relaxed motor threshold in the first dorsal interosseus (1DI). Importantly, the participants were unaware of the TMS-

intensity that would be used in each trial. In both voluntary and involuntary conditions, a physically comparable movement of the left hand preceded the somatic effect. However, only in the voluntary condition did the subject intentionally cause the somatic effect.

As in experiment 2.1, the voluntary action or passive involuntary movement were performed with the left hand, and the somatic effect was experienced in the right hand, separated. Across both operant conditions, the somatic effect occurred 270 ms after the key-press.

TMS was delivered using a figure-of-eight coil with a Magstim 200 stimulator (Whitland, UK). The optimal location for producing twitches (MEPs) in the right 1DI muscle was located by systematically exploring a 1-cm grid over the hand area of the left motor cortex. The motor threshold (MT) was calculated for each subject by reducing stimulator output in 5% steps to find the lowest level at which three MEPs exceeding 50 mV peak amplitude were obtained from five successive stimulations of the relaxed 1DI. Thresholds ranged from 30% to 50% of stimulator output (mean, 40%). Three different TMS output levels were used throughout the experiment: 110%, 130% and 150% of relaxed motor threshold. Ten trials at each output level were used in each block. The level was changed every five trials, using a different random order of levels for each block and each subject. EMG was measured from the 1DI muscle of the right hand with bipolar recording from surface Ag/AgCl electrodes, amplified and digitised at 5 kHz.

The same 12 naïve volunteers, who participated in Experiment 2.1, took part in this experiment, shortly after Experiment 2.1. Procedures were approved by the institutional ethics committee and participants gave their informed consent to participate in this study. Other aspects of method were the same as in Experiment 2-1.

2.3.3. Results

Peak-to-Valley MEP size was measured for each trial. Mean MEP sizes and mean subjective intensity ratings across conditions are shown in Table 2-4.

Table 2-4 Mean MEP size and Mean Subjective Ratings across conditions.

	Single-event Baseline Condition	**Voluntary Context**	**Involuntary Context**
TMS at 110% of MT			
Mean MEP size in mV (*SD*)	**1.12** (*0.59*)	**0.87** (*0.56*)	**1.07** (*0.78*)
Mean Subjective Rating (*SD*)	**2.44** (*1.13*)	**1.52** (*0.43*)	**2.48** (*1.19*)
TMS at 130% of MT			
Mean MEP size in mV (*SD*)	**1.77** (*0.63*)	**1.80** (*0.75*)	**1.57** (*0.72*)
Mean Subjective Rating (*SD*)	**4.28** (*1.90*)	**3.49** (*1.38*)	**4.37** (*2.13*)
TMS at 150% of MT			
Mean MEP size in mV (*SD*)	**2.40** (*0.63*)	**2.18** (*0.71*)	**2.33** (*0.84*)
Mean Subjective Rating (*SD*)	**6.54** (*2.27*)	**5.83** (*2.08*)	**6.30** (*2.21*)
Mean			
Mean MEP size in mV(*SD*)	**1.76** (*0.49*)	**1.62** (*0.64*)	**1.66** (*0.73*)
Mean Subjective Rating (*SD*)	**4.42** (*1.63*)	**3.61** (*1.26*)	**4.38** (*1.93*)

Because the main interest of this study was on the effect of agency, the analysis focused on the comparison between the voluntary and the involuntary conditions. However, the fact that the MEPs were largest in the single event control condition rules out the possibility that the somatic effect was facilitated by any spread of neural activation associated with the action of the left hand. The mean ratings were subjected to

factorial ANOVA, using two within-subject factors. These were the sensorymotor context (voluntary vs. involuntary) and the TMS-output used (110%, 130%, 150%). Unsurprisingly, the TMS output had a significant effect on the rating ($F(2,22)=74,6$, $p<0.001$). More interestingly, the main effect of sensorymotor context was also significant ($F(1,11)=8.067$, $p<0.02$) suggesting that the somatosensory consequences generated by a voluntary action are perceived as less intense than when they follow a passive involuntary movement. However, no significant interaction between these two factors was found ($F(2,22)=0.988$, $p>0.05$), suggesting that TMS strength modulated the perceived intensity equally in both conditions. This result suggests that a voluntary action reduced the perceived intensity of somatic effects by a fixed amount, rather than attenuating them in proportion to their size, in the manner of a linear gain coefficient.

To investigate whether these results could arise from a reduction in actual MEP size we analysed the mean MEP size using the same factors. As predicted, the effect of TMS output level was highly significant ($F(2,22)=74.811$, $p<0.001$). Importantly, the effect of operant context was not significant ($F(1,11)=.0.58$, $p>0.05$), but the interaction of the two factors was significant ($F(2,22)=5.643$, $p<0.01$). The interaction arose because MEPs were slightly larger after voluntary action than after involuntary action at the middle level of TMS output (see Table 2-4). In brief, the physical variation in MEP size could not explain the monotonic changes in intensity rating.

In order to test the main effect of the sensorymotor context, the mean MEP sizes and the mean subjective ratings were pooled across all levels of the TMS output factor. These means are shown in Figure 2-7.

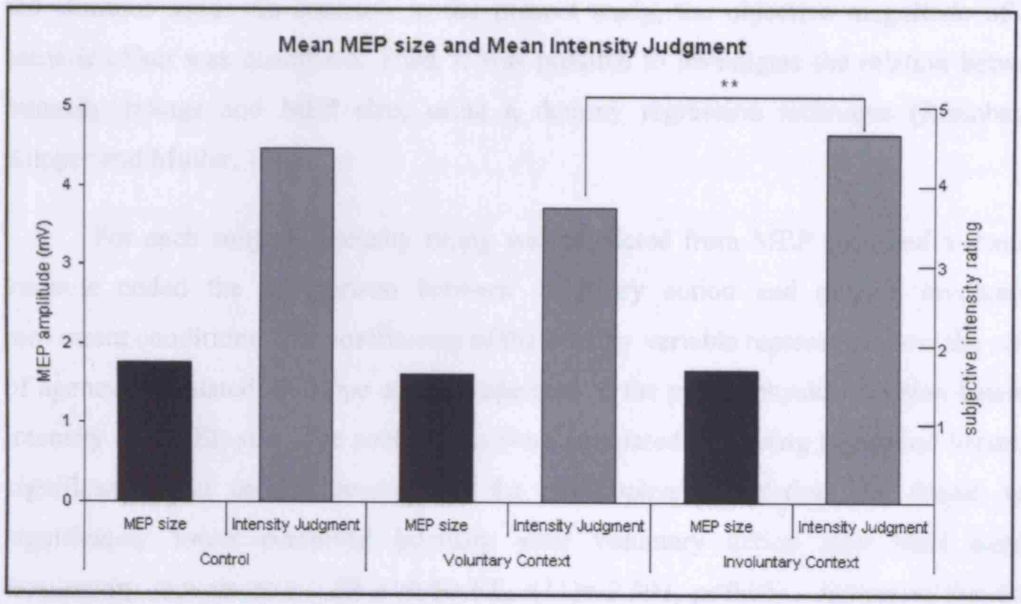

Figure 2-7 Mean MEP size and Mean Subjective Intensity Rating

A simple effects analysis (Howell, 1977) was used to compare the subjective intensity ratings between voluntary and involuntary conditions. The difference was significant ($t(11)=2.51$, $p<0.005$). The MEP sizes between voluntary and involuntary conditions were not significantly different ($t(11)=.24$, $p>0.05$).

Overall, the analysis suggests that the differences in the subjective intensity ratings were due to the different sensorymotor context (voluntary vs. involuntary) and not due to differences in the MEP size or the TMS-output. Identical somatosensory consequences were perceived as less intense when caused by a voluntary action than when caused by an involuntary movement, suggesting that the perceived intensity of a somatic effect is modulated by a self-generated action.

Relation between perceived intensity and MEP size

A follow-up analysis investigated how sensory suppression occurs. Does it act as a proportional attenuator, or does it shift perceived intensity of all somatic effects by a fixed amount? This question was addressed by regressing the perceived intensity on the objective MEP size, and investigating whether the slopes or intercepts of this regression changed across conditions, using dummy regression analysis. Previous studies have

either used a single, unvarying somatosensory stimulus, or have not precisely quantified the stimulus used. In contrast, in the present study, the objective magnitude of the somatic effect was quantified. Thus, it was possible to investigate the relation between intensity ratings and MEP size, using a dummy regression technique (Kleinbaum, Kupper and Muller, 1988).

For each subject, intensity rating was predicted from MEP size, and a dummy variable coded the comparison between voluntary action and passive involuntary movement conditions. The coefficients of the dummy variable represented how the effect of agency modulated the slope and the intercept of the psychophysical relation between intensity and MEP size. The coefficients were compared to 0 using two-tailed t-tests. A significant effect on the intercept of the psychophysical relation was found, with significantly lower perceived intensity after voluntary action than after passive involuntary movement (–1.19 +/-0.50 SE, $t(11)$=-2.391, p<0.05). However, the slope coefficients did not differ significantly between voluntary and involuntary condition (0.26 +/-0.27 SE, $t(11)$=.958, p>0.05).

Therefore, agency shifted the perceived intensity of all subsequent somatic effects by a fixed amount, but it did not attenuate percepts in the manner of a gain. This analysis confirms a similar finding from the previous ANOVA analysis.

2.3.4. Discussion

Experiment 2.2 showed that sensory attenuation was due to the voluntary context of the preceding movement and not due to the existence of a prior movement *per se*. More importantly, self-generated somatic effects, whose magnitude cannot be predicted by the forward model of the motor system, were still attenuated. This suggests that efference was a sufficient condition for the modulation of the perceived intensity of self-generated effects, possibly because these were predictable across time. In fact, the results suggest that whenever a somatic effect is self-generated, a sensory *suppression* in the perception of somatic effect occurs.

In one of the early studies on sensory attenuation, Weiskrantz et al. (1971) suggested that sensory attenuation occurs as a result of a general "gating" of all incoming stimulation *during* self-generated movements. On this view, sensory gating occurs when sensory stimulation is contemporaneous with the movement. In the present study the effect occurred 270ms after the self-generated movement. Therefore, it seems unlikely that the co-occurrence of the movement with the re-afference generated the observed sensory suppression.

The results from this experiment also recall previous studies. Blakemore and colleagues (1999) found lower perceived intensity for self-generated stimuli than for externally imposed stimuli. More recently, Shergill and colleagues (2003) investigated the perception of force escalation. The study replicated the basic phenomenon of sensory attenuation of self-produced stimulation. In a control experiment, Shergill and colleagues used a set-up somewhat similar to the present experiment. Subjects experienced a brief constant force to the tip of their left index finger. They were then asked to use their right index finger to match the perceived force, by pushing on their left index finger through a force transducer. In this condition, they consistently overestimated the force required, suggesting that self-generated forces are perceived as weaker than externally-generated forces of the same magnitude. In a second condition, subjects were again asked to match the experienced force, this time by using their right index finger to move a joystick that controlled the force output of the torque motor. In this condition, as in our experiment, the right hand does not generate the sensory effect directly, and predictive mechanisms are not activated. The results showed that in this latter condition, the reproduced force

matched more accurately the original force, suggesting that sensory attenuation did not occur, compared to the first condition. However, the authors did not directly compare this second condition to a condition in which the second stimulus would be either passively-generated (as in the present study) or externally-generated. Thus, their finding does not contradict the present finding of a general sensory suppression occurring following self-generated stimulation.

The present study replicated the basic phenomenon of sensory attenuation, with the additional control that the somatic effects were always preceded by a physical identical movement. Blakemore and colleagues (Blakemore, Frith & Wolpert, 1999) suggested that the attenuation they observed is proportional to sensory discrepancy, that is, the error between the sensory feedback predicted by the forward model and the actual sensory feedback produced by the movement. This is the 'proportionality hypothesis'. On a strong version of this view, the perceptual intensity of an event should be linearly proportional to the difference between its predicted and actual sensory consequences.

In the present experiment, the sensory discrepancy was additionally varied by the TMS output level. Subjects' best estimate of the somatic effect was presumably an average-sized MEP. If awareness is reconstructed based on sensory discrepancy, shifts in perceived intensity of the somatic effect should be proportional to the size of the MEP. However, no such proportional effects were found. Dummy regressions showed that voluntary action adjusted the offset level (intercept) but not the gain (slope) of perceived MEP intensity. These data offer no support to a proportional relation between awareness and sensory discrepancy.

Thus, self-generated actions seem to shift the perceived intensity of all subsequent somatic effects by a fixed amount, but they do not attenuate percepts in a proportional manner. It is due to the operation of the forward model that sensory events are attenuated in a proportional manner, because of the detailed comparison between motor parameters, predicted and actual sensory feedback. However, the present study suggests that it is due to the presence of efference *per se* that sensory events are suppressed, because the amount of sensory discrepancy does not influence the amount of attenuation. The critical contribution of efferent information in the generation of the observed sensory suppression may be accounted by the temporal information that efference carried. In the voluntary condition, efferent information could not predict the

magnitude of the somatic effect, but it could predict the onset of the action that would lead to the somatic effect. Temporal predictions seem to be critical for the perception of self-generated effects (see also Blakemore, Frith & Wolpert, 1999; Haggard,Clark & Kalogeras, 2002). Thus, this temporal prediction could result in the modulation of the perceived intensity, in a way similar to the modulation of the perceived time of the occurrence of a somatic effect that was self-generated (see Experiment 2.1, and section 2.4).

It has been suggested that sensory attenuation may be an important index of agency and selfhood (Blakemore & Frith, 2003; Blakemore, Wolpert & Frith, 2002). On that view, self-ascription of actions is not a predictive process based on the presence of the efference copy, but a verificational process of comparing the predicted with the actual outcome. The results of Experiment 2.2 showed that an effect similar to sensory attenuation of the perceived intensity of self-generated effects might occur even when the comparison between the predicted and the actual intensity is not accurate. Thus, it is suggested that the sense of agency could arise at an early stage in the planning of action, and before the precise details of the impending sensory effects are determined within the forward model. The intention to act and the presence of efference would therefore be sufficient to generate a sensory suppression effect. Thus, efference could serve as a primary index of ownership of action, arising in advance of the sensory feedback.

2.4. General Discussion: Agentic modulation of time and intensity judgments

In Experiments 2.1 and 2.2, the main focus was on the way the brain links voluntary actions to their subsequent somatic effects. The design compared somatic effects of agentic movement to those of non-agentic movement: a voluntary action and its somatic effect were contrasted to an involuntary passive movement and an identical somatic effect. The parameters of movement were identical (a key press) across conditions, and the "causal" relation between the key press and the TMS pulse was also identical. Only the authorship of the action was different across conditions. This is the first time that the perceived effects of voluntary actions are compared to the sensory effects following an identical movement performed either voluntarily or involuntarily. Experiment 2.1 studied the time-awareness of these events under these conditions, while Experiment 2.2 studied variations in the perceived intensity of the somatic effect.

The results showed that both the time-awareness and the sensory perception of these events are modulated by the agentic nature of the action that caused them. The awareness of the voluntary actions and their somatic effects differs dramatically from the awareness of physically-equivalent movements and subsequent somatic effects which are imposed involuntarily on the body. In Experiment 2.1, participants perceived voluntary actions as occurring later and their bodily effects as occurring earlier in the agency context, compared to single-event baseline conditions. When the voluntary action was replaced by a passive, involuntary movement this attraction effect reversed. Thus, time-awareness of voluntary actions and their subsequent somatic effects is characterized by an intentional binding effect. In Experiment 2.2, subjects rated the intensity of the same kind of TMS-induced somatic effect, again following a voluntary action or a passive movement. When the somatic effect was caused by a voluntary action, it was perceived as significantly less intense than when it followed a passive movement.

Perceptual shifts in time and intensity judgments

In a final exploratory analysis, the time and intensity judgements from the 2 experiments were combined in a multivariate analysis, with a single factor of operant context (voluntary action vs. involuntary movement). This analysis aimed to show whether agency effects were more pronounced on time or on intensity judgement. There

was a significant difference between perceptions of somatic effect after voluntary action and after passive movement ($F(2,10)=5.37$, $p=0.026$). This was expected given the univariate ANOVA results of Experiments 2.1 and 2.2. The present analysis focussed on the standardised canonical coefficients (SCCs), which express the extent to which this between-condition difference is seen in the two dependent variables. The SCCs showed similar loadings on timing judgements (*1.887*) and on intensity judgements (*1.478*), implying that both these dimensions of perception may be modulated to an equivalent extent by agency context. This suggests that the perceptual shifts observed in time and intensity perception are possibly the consequences of a common mechanism constructing the experience of agency.

In summary, both the perceived timing and the perceived intensity of somatic effects are shifted following a voluntary action. These shifts are not found following passive involuntary movement. Do these shifts represent a change in the bias or the offset level of a psychophysical coupling, or do they represent an adjustment that is proportional to the sensory discrepancy?

According to the proportionality hypothesis (Blakemore, Frith & Wolpert, 1999), the percept is linearly proportional to the error signal or sensory discrepancy between predicted and actual feedback. This is a key prediction of any comparator-based model of agency (see Section 1.2.4.2). The observation of both perceptual attraction and repulsion effects in experiment 2.1 might initially seem consistent with the proportionality hypothesis. The perceptual repulsion between passive involuntary movements and their somatic effects might reflect the operation of an inverse binding, whose function is to separate in time, and thus to discriminate, pairs of events that cannot be attributed to our own causal agency. A single neural mechanism, based on a predictive forward model, could generate a range of conscious experiences varying along a continuum from perceptual attraction to perceptual repulsion. The shift in awareness could be directly proportional to the discrepancy between predicted and actual sensory events in the forward model. Since the sensory discrepancy is not calculated until after delayed feedback is available, this view implies that the awareness of our actions is reconstructed post hoc, rather than generated as part of the process of intending and generating the action. If awareness is reconstructed based on sensory discrepancy, shifts

in perceived time (Experiment 2.1) or perceived intensity (Experiment 2.2) of the somatic effect should be proportional to the size of the MEP.

Across both experiments, the sensory magnitude of the somatic effects was not predicted by the action that caused them. In fact, the efference copy of the voluntary action could only predict the onset of the self-generated movement that would eventually cause the somatic effect 270ms later. Thus, given that efference carried a pure temporal signal, it could have been directly used to predict the onset of the event, without the contribution of the forward model. This raw temporal efferent signal could be generating the observed shifts in the perceived time and the perceived intensity of these somatic effects.

In addition, in the present experiments, the sensory discrepancy was additionally varied by the TMS output level. Subjects' best estimate of the somatic effect presumably involved a typical MEP. Thus, if the forward model of the motor system were used to modulate the perception of the somatic effects, the predicted typical MEP would almost always differ from the actual MEP, whose size was under experimental control. In experiment 2.1, shifts in perceived time were not proportional to MEP size. In experiment 2.2 dummy regressions showed that voluntary action adjusted the offset level (intercept) but not the gain (slope) of perceived MEP intensity.

Overall, the results suggest that intention acts as a general context for awareness, shifting perceived time and perceived intensity by fixed amounts. Experiments 2.1. and 2.2 found a general contextual modulation of perception across time- and sensory-awareness of somatic effects that are voluntarily self-generated. This shifting may reflect a contextual modification of awareness, and need not involve the function of a parametric forward model. This context effect could be applied in the form of a 'sensory bias'. This bias occurs quite generally, even when the details of the action do not predict the details of its sensory consequences. It is as if the system tags the forthcoming event as being "mine", before the motor system starts predicting and correcting the various sensory-motor parameters of the movement. This sensory bias is expected to be present whenever a sensory consequence can unambiguously be attributed to oneself. It is also suggested that the mere presence of intention and efferent information suffice for this sensory bias to be generated. Possibly, the role of efference in the present experiment is

to generate an accurate temporal signal that denotes the onset of the events (e.g. action) that will lead to the generation of the somatic effect.

This finding is not contradictory to the functional role of the forward model. It simply suggests that in the case of self-generated actions, the movement is tagged as "mine" by virtue of the presence of efference. If there is more information available for a detailed processing of the sensory outcome, then the forward model will produce accurate predictions. The discrepancy between predicted and actual outcome will function in a proportional manner in the resulting perceptual attenuation, whereas the sensory bias derived from efference seems to function as general contextual modulation, because the perceived intensity of all subsequent somatic effects shifted by a fixed amount. This context effect could be applied predictively, as soon as the intention is translated to an appropriate motor command, rather than post hoc, and may reflect the functional role of the efference copy as an index of authorship.

In the next chapter, Experiment 3.1 will investigate the specific role of efferent information in the explicit experience of self-recognition.

3. Recognizing the Bodily Self: the role of efference[2]

3.1. Introduction

Imagine that you are entering into a hall, where a mirror, large enough to reflect many people, is just in front of you. It is not easy to locate the reflection of your own self among those of others. Most people would make a gesture and try to visually locate it in the reflecting mirror. In other words, they would produce a movement and compare it against the visual feedback in order to recognise themselves. This example illustrates the interplay between central (i.e. efferent) information related to the motor command, and afferent information, in this case visual, related to sensory feedback of movement in self-recognition.

Recent research on self-recognition (for a review see Jeannerod, 2003) distinguishes between two related computational problems: the problem of action recognition and the problem of self-recognition. Self-recognition, in the current context, involves deciding whether a visual stimulus shows one's own body or not. Thus, self-recognition is also possible in the absence of any movement or action, for example by purely morphological features. In action-recognition, the brain must distinguish between afferent information generated by our own movements, and afferent information that is externally imposed. Action-recognition may involve unconscious operation of internal predictive models of the motor system (Blakemore & Frith, 2003; Blakemore & Sirigu, 2003), while self-recognition appears to be a specific cognitive process typically involving conscious experience (Daprati et al., 1997).

As the example at the beginning of this chapter shows, we often use voluntary movements as a means of self-recognition. This fact by itself suggests a hierarchical relation between action-recognition and self-recognition: voluntary action can aid self-recognition only if one can be sure that the viewed resulting body movements were caused by one's own voluntary action. In most studies of self-recognition, participants see a body-part, which may or may not be related to their own body. The task is to judge whether what they see is their own body or not. The information available to support this judgment is systematically varied across conditions, for example by moving the hand

[2] Experiment 3.1 was performed in collaboration with Angela Sirigu, Nelly Mainy, Nicolas Franck and Patrick Haggard. This study was published in Tsakiris M, Haggard P, Franck N, Mainy N & Sirigu A (2005). A specific role for efferent information in self-recognition. *Cognition*, **96**(3), 215-231.

(Daprati et al., 1997; Sirigu et al., 1999), by introducing delays between the movement and the visual feedback (Franck et al., 2001), or by rotating the hand image (Van den Bos & Jeannerod, 2002). Self-recognition requires the monitoring and integration of various sources of information such as intention, motor command and somatic perception in a short time-window. As discussed in Chapter 2, an internal model of the motor system such as the forward model may be used for self-recognition because it can detect conflicts between the predicted and the actual sensory feedback.

Only a few studies have explicitly investigated the link between voluntary movement and action-recognition (Farrer et al., 2003; McDonald & Paus, 2003), while no studies have specifically addressed the role of voluntary movement for self-recognition (see Table 3-1).

Table 3-1 A summary of recent experiments on action- and self-recognition

Summary of Action-Recognition Studies

	Fourneret & Jeannerod, 1998	**Farrer et al., 2003b**	**MacDonald & Paus, 2003**
Participants	Normal Subjects	Normal Subjects & Deafferented Patient GL	Normal Subjects
Experimental Manipulation	Angular Bias	Angular Bias	Temporal Delays
Visual Feedback	Display of the line drawn by the subjects	Computer-reconstructed image of a hand	CyberGlove
Manipulation of Efference	No	Yes	Yes
Results	Subjects automatically compensate for the introduced bias, but they are unaware of these corrections when bias<15°.	Normal subjects: differences between active and passive movement were significant only for bias >30°. GL was significantly more impaired.	rTMS over left superior parietal lobule impaired the detection of asynchrony for active but not for passive movement.

Summary of Self-recognition Studies

	Daprati et al., 1997	**Sirigu et al., 1999**	**Van den Bos & Jeannerod, 2003**
Participants	Schizophrenics & Controls	Parietal Patients & Controls	Normal Subjects
Experimental Manipulation	Visual Feedback: 1.Own hand 2. Other's hand/same movement 3. Other's Hand/different movement	Visual Feedback: 1.Own hand 2. Other's hand/same movement 3. Other's hand/different movement	Visual Feedback : 1. Rotation of Hand-Location on screen (0°, 90°, -90°, 180°) 2. Movement (same, different, no movement)
Visual Feedback	Video display of 1 hand	Video display of 1 hand	Video Display of 2 hands (performing same/different/no movement)
Manipulation of Efference	No	No	No
Results	Schizophrenics were significantly impaired when they saw other's hand performing same movement	Parietal patients were significantly impaired when they saw other's hand performing same movement	When movements were the same, self-recognition performance was influenced by the rotation of the hand image.

The summary of studies presented in Table 3-1 shows that only two action-recognition studies have dissociated efferent from afferent information, while none of the self-recognition studies have examined the distinctive roles of efferent and afferent information. In fact, most self-recognition studies have focused on the self-recognition ability of schizophrenics and parietal patients, because of the deficits these groups show in action attribution (Blakemore et al., 2000) and action recognition (Fourneret et al., 2001; Franck et al. 2001; Schwoebel et al., 2002).

Daprati et al. (1997) and Sirigu et al. (1999) investigated the perception of simple and complex gestures in schizophrenic and in parietal patients respectively. These two studies had same experimental designs. Participants were instructed to perform simple or complex self-generated movements (extension of one or two fingers), without direct visual image of their hand. Participants could see on a mirror in front of them (a) their own hand, or (b) the experimenter's hand performing the *same* movement as the participant's hand, or (c) the experimenter's hand performing a *different* movement from the participant's hand. Participants were asked to judge whether they saw their hand or not. The pattern of results was the same across these two experiments. Patients and

controls performed almost perfectly when they saw their own hand, and when they saw the experimenter's hand performing a *different* movement. This suggests that the detection of a mismatch between visual and proprioceptive/efferent information is a relatively easy task, even for patients who display impaired awareness of action (for a review see Frith, Blakemore & Wolpert 2002a,b). However, both schizophrenics and parietal patients were significantly worse, compared to controls, when they saw the experimenter's hand performing the *same* movement as them. In this case, they said that they saw their own hand, whereas in fact they saw the experimenter's hand. In other terms, participants tended to misattribute the experimenter's hand to themselves, that is,

In all these studies (Daprati et al., 1997; Sirigu et al, 1999; see also van den Bos & Jeannerod, 2002), the performed movements were self-generated, that is, participants had both efferent and afferent signals available for comparison against the visual feedback. Efferent information was not dissociated from proprioceptive information, and therefore the relative contributions of these two kinds of information about explicit self-recognition were not clarified. Results showed a significant impairment in the self-recognition performance of schizophrenic and parietal patients when these groups saw someone else's hand performing the *same* movement as they did. In fact, patients misattributed the viewed hand to themselves. What can account for the enhanced performance of normal participants? These studies cannot conclusively answer whether normal subjects integrated in a more efficient way afferent information (visual and proprioceptive feedback), or whether they used efferent information for their self-recognition judgments.

The specific contribution of efference to self-recognition can only be addressed by implementing a situation where proprioceptive information is constant, while efference is systematically manipulated. This can be empirically addressed in a study that will selectively manipulate efferent information. To do so, it is necessary to compare self-recognition performance between a condition where efferent information is present and a condition where efferent information is absent: for example by comparing recognition of movements which are either active or passive (i.e. they either include or lack efferent information), while maintaining afferent information similar, as shown in Figure 3-1.

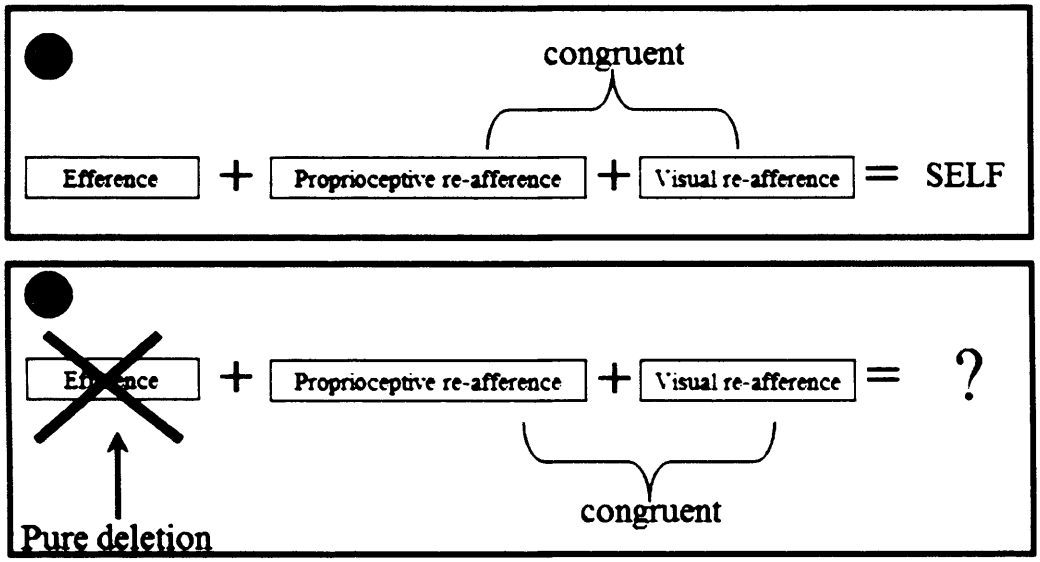

Figure 3-1 The "deletion of efference" hypothesis. In the studies by Daprati, Sirigu and colleagues, across all conditions, both efferent and afferent information (i.e. proprioceptive and visual) could be used for the self-recognition judgment. In the critical condition where participants saw the experimenter's hand performing the same movement (see box 1), the visual feedback was congruent to the proprioceptive feedback, and efferent information predicted a congruent movement. In order to study he specific role of efferent information it is necessary to design a situation where the efferent information will be absent from this equation. Thus, the direct comparison of the condition presented in box1 to the condition presented in box 2 will show the specific contribution of efferent. One way to implement this comparison in an experimental set-up is to compare self-recognition of bodily movements that self-generated to the self-recognition of similar bodily movements that are externally-generated.

The aim of the Experiment 3.1 was to investigate the specific contribution of efferent information in self-recognition. Unlike previous studies, the present study systematically manipulated the availability of efferent information for self-recognition judgements by spatially dissociating an action from its bodily effect (see Chapter 2). Thus, the action was separated from the somatic effect by localizing them on different body-parts. Subjects made voluntary actions with their left hand, which were transmitted by a lever to the passive right hand. Self-recognition judgements were based on vision of the right hand only, which was either the subject's own hand, or someone else's hand. More importantly, efferent information was manipulated. The action could be either self-generated or externally-generated. In the self-generated condition, participants moved

their right hand by an active movement of their own left hand, in which case both efference and afference were present. In the externally-generated condition, the experimenter used the same lever to move the participants' right hand. In the latter case only afferent information was available to the subject. Therefore, the availability of efference from the left hand was manipulated, while proprioceptive input from the right hand was constant across conditions, independently of the movement that caused it (self- or externally generated). This design enabled the assessment of the specific role of efferent information in a self-recognition task.

This dissociation allowed the investigation of the signals used during self-recognition: does the recognition of the somatic effect depend primarily on the afferent information (i.e. comparison between vision and proprioception) generated during the body movement itself, or does it also depend on efferent information from the spatially remote action that produced this somatic effect?

3.2. Experimental Design, Methods and Participants

Experimental Design

The experimental design was 2×2 factorial. The factors were (i) the authorship of action (self-generated/externally-generated), and (ii) the identity of the viewed hand (own hand/other's hand).

(i)Authorship of Action: This factor had two levels. The action could be either self- or externally-generated. The action was to press with the left index finger on the left side of a lever (length 15 cm, angle 45°). This action lifted the subject's right index finger, which rested on the right end of a lever (see Fig. 3-2). The lever could be pressed either by the subject ('self-generated' condition) or by the experimenter ('externally-generated' condition). In the self-generated condition, participants moved their right hand by an active movement of their own left hand, in which case both efference and afference were present. In the externally-generated condition, the experimenter used the same lever to move the participants' right hand. In the latter case only afferent information was available to the subject. This manipulation controlled for the presence or absence of efferent information.

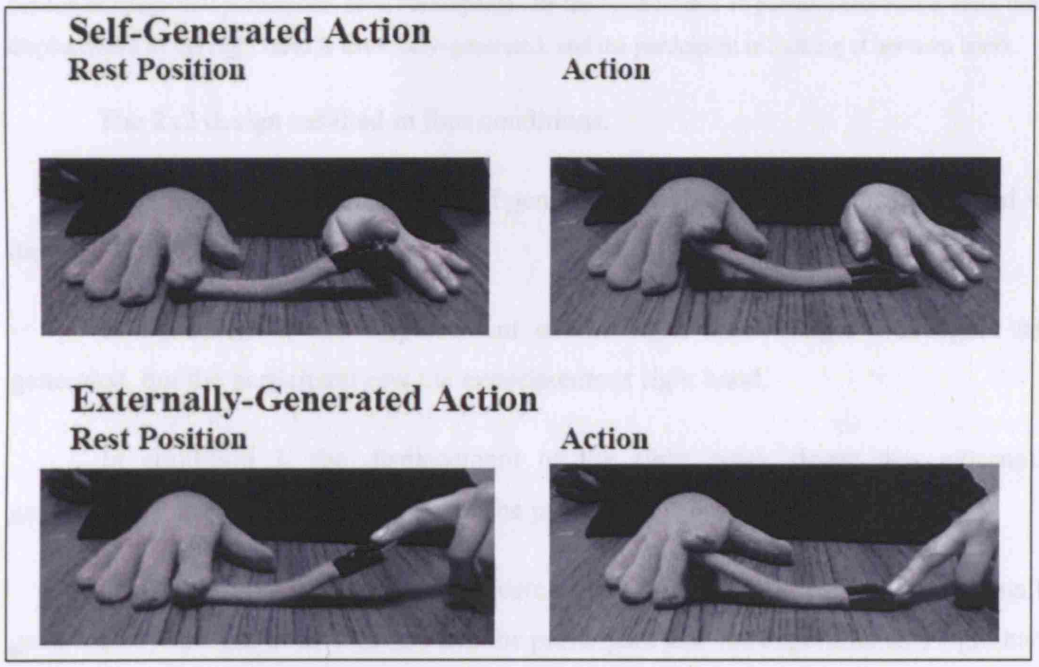

Figure 3-2 An illustration of the self- and externally-generated conditions.

(ii) Identity of the Hand: This factor, related to the manipulation of visual feedback, had two levels. Subjects viewed either their own right hand undergoing a passive displacement ('view own hand' condition), or someone else's right hand ('view other's hand' condition) undergoing the same passive displacement. Visual feedback was limited to the presentation of the right hand and the right side of the lever only. The left hand and the left end of the lever were never seen. To prevent self-recognition based on purely morphological characteristics, both the subject's hand and the other person's hand were covered with identical woollen gloves, positioned on identical levers. Figure 3-3 shows 1st person perspective from which participants saw the presented right hand.

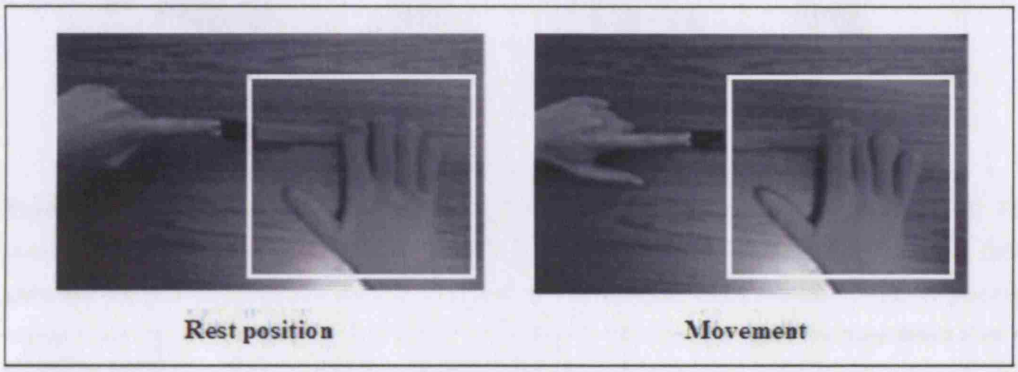

Figure 3-3 Visual feedback was limited to the presentation of the right hand only. The white square is the actual image that participants saw. Participants saw the hand from a 1st person perspective. Here the displacement of the right hand is externally-generated, and the participant is looking at her own hand.

The 2x2 design resulted in four conditions:

In condition 1, the subject herself generated the right hand displacement, and saw her own right hand.

In condition 2, the displacement of the right index finger was again self-generated, but the participant saw the experimenter's right hand.

In condition 3, the displacement of the right index finger was externally-generated by another experimenter, and the participant saw her own right hand.

Finally, in condition 4, the displacement of the right index finger was externally-generated by another experimenter, and the participant saw the experimenter's right hand. These conditions are schematically presented in Figure 3-4.

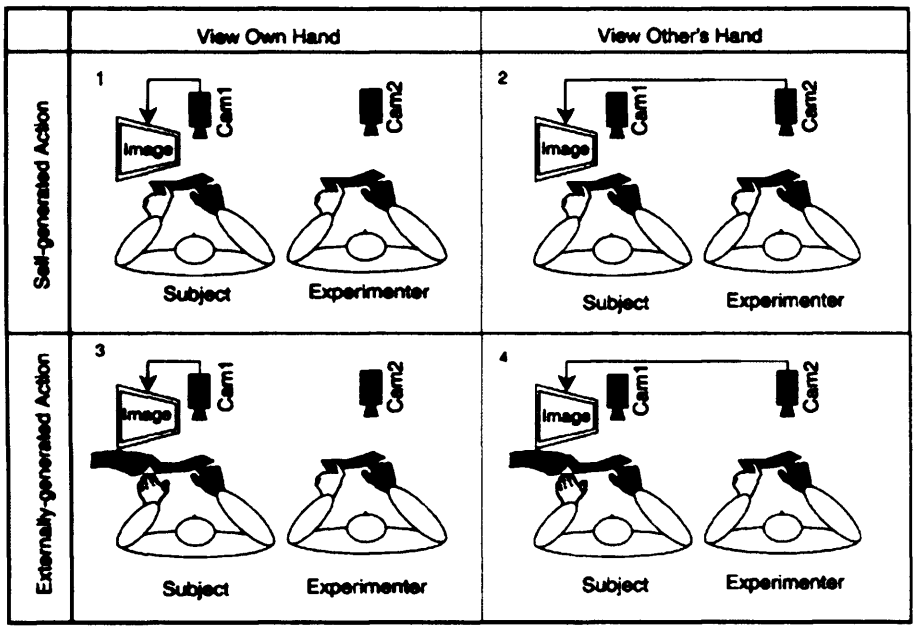

Figure 3-4 A schematic representation of the 4 experimental conditions in Experiment 3.1. The conditions were arranged as a 2×2 factorial design with factors of the authorship of action (self-generated vs. externally-generated), and the source of the visual feedback available to the subject (the subject's own right hand vs. the experimenter's right hand). The participant did not have direct view of her hands. The displacement of the right index finger was always passive.

Methods

Subjects performed four blocks in total. The "authorship of action" factor was blocked, whereas the visual feedback was manipulated randomly within blocks. Two blocks for the 'self-generated' condition were performed, followed by two blocks for the 'externally-generated' condition or vice versa. The order of blocks was counterbalanced across subjects. Each block contained 30 trials, with 15 trials for each visual feedback condition occurring in a random order. After each block there was a short break. Before the experiment, each subject performed two training blocks of 10 trials each, one for the self-generated movement and one for the externally-generated movement, to familiarize themselves with the apparatus and the procedure. Participants did not receive feedback.

Each participant sat in cabin with her hands on a table, while an experimenter sat at a separate but similar table (see Figure 3-5). Two video cameras filmed the participant's and the experimenter's right hands. Either camera could be routed via a

computer to a video display. The video display was reflected on a mirror placed on the table in front of the participants. Thus, the participant saw the presentation of the hand in front of her from a 1st person perspective. A video switch controlled which camera was routed to the display. Black and white video images were displayed. The delay in relaying the image was less than 20 ms. Thus, the participant could see either her right hand or the experimenter's right hand at the centre of the mirror.

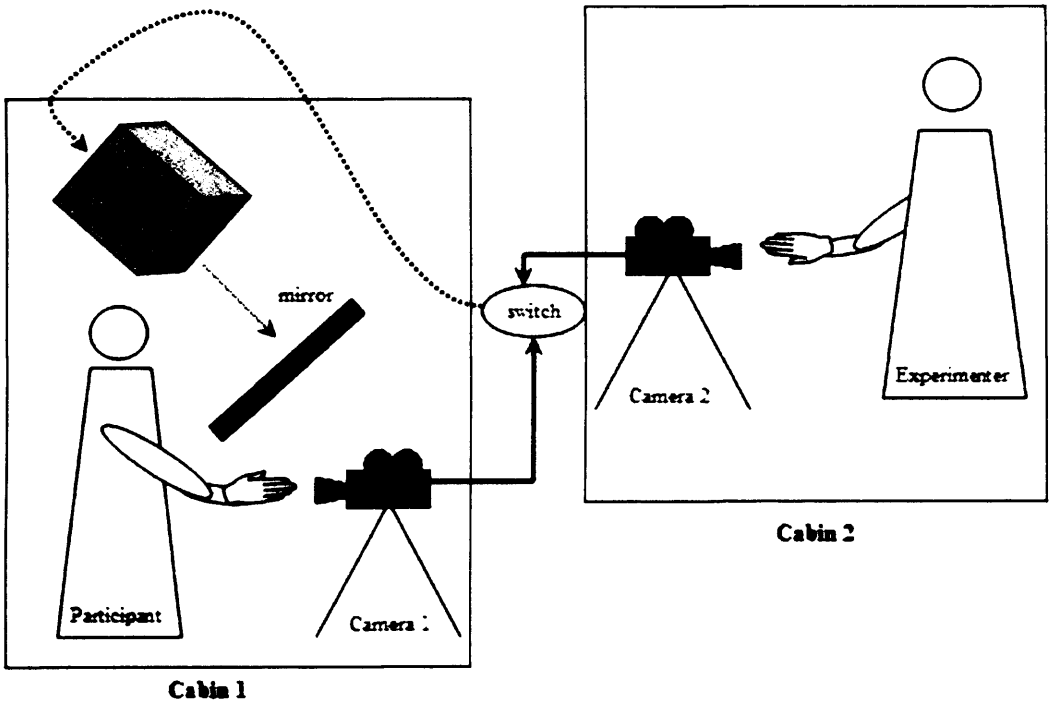

Figure 3-5 The experimental set-up used in Experiment 3.1

A further experimenter was continually checking two TV monitors, connected to the two cameras respectively. This experimenter could check that the participant and the other experimenter made comparable movements at similar times. This discouraged the participant from deliberately making slow or otherwise idiosyncratic, and thus highly recognisable movements. Trials in which the experimenter detected an obvious difference between the onset times of the participant's movement and the other experimenter's movement were noted and excluded from analysis. 500 ms after the onset of the image, an auditory tone gave the signal for the execution of the action, and the hand remained on the screen for a further 1500 ms more. This brief display was chosen in order to minimize the time available to study any morphological differences. At the

end of each trial, the forced choice options (Yes/No) appeared on the mirror (see Figure 3-6. Participants had to respond verbally 'Yes' if they thought they saw their own right hand, and 'No' if they thought they saw someone else's hand. Subjects were instructed to respond promptly.

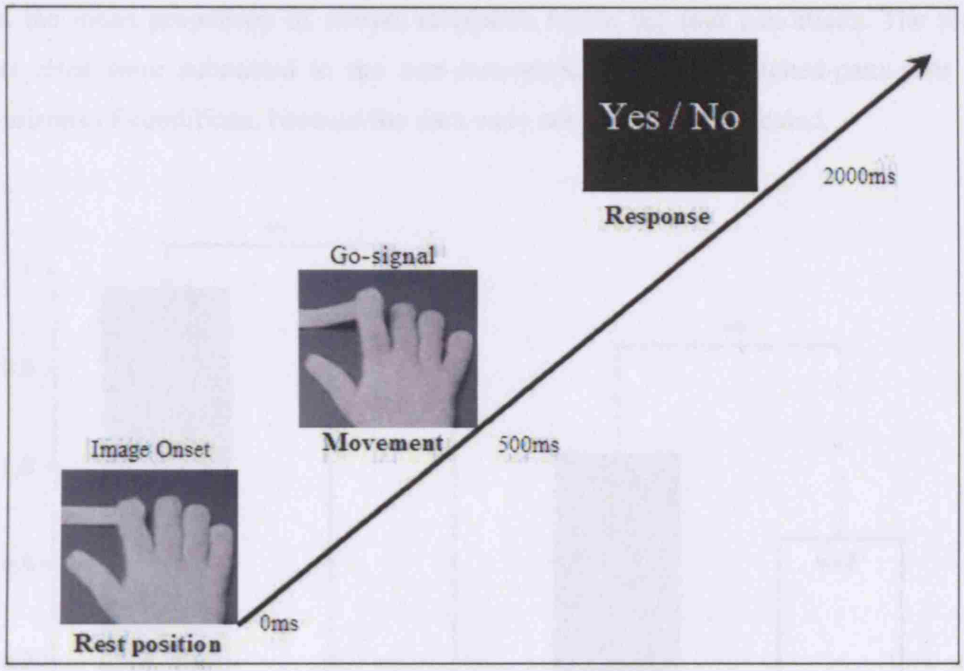

Figure 3-6 The time sequence of events during the experimental trials.

Participants

Eighteen naïve volunteers, with normal or corrected to normal vision, took part (mean age 24.1, 10 female). All participants were right-handed. Mean laterality coefficient, as assessed by the Edinburgh Inventory (Oldfield, 1971), was +0.87 (SD=0.13). None of the subjects suffered from neurological or psychiatric pathologies. All participants gave their informed consent to participate in this study.

To summarize, the experiment compared self-recognition performance across four conditions that differed according to the authorship of the action (Self-generated/Externally-generated) and the visual feedback of the effect of action (Own hand/Other's hand). Note that across all conditions and trials what the subject sees and feels is a displacement of the right index finger. Across all conditions and trials, the afferent information originating from their right hand was held constant, but efferent information was available only in the self-generated condition.

3.3. Results

Due to unsuccessful performance in the execution of the action, such as a gross asynchrony in the initiation of the subject and the experimenter's action detected on-line by an additional experimenter, 3.1% of trials were excluded from analysis. Figure 3-7 shows the mean proportion of correct responses across the four conditions. The mean correct rates were submitted to the non-parametric Wilcoxon matched-pairs-tests for comparisons of conditions, because the data were not normally distributed.

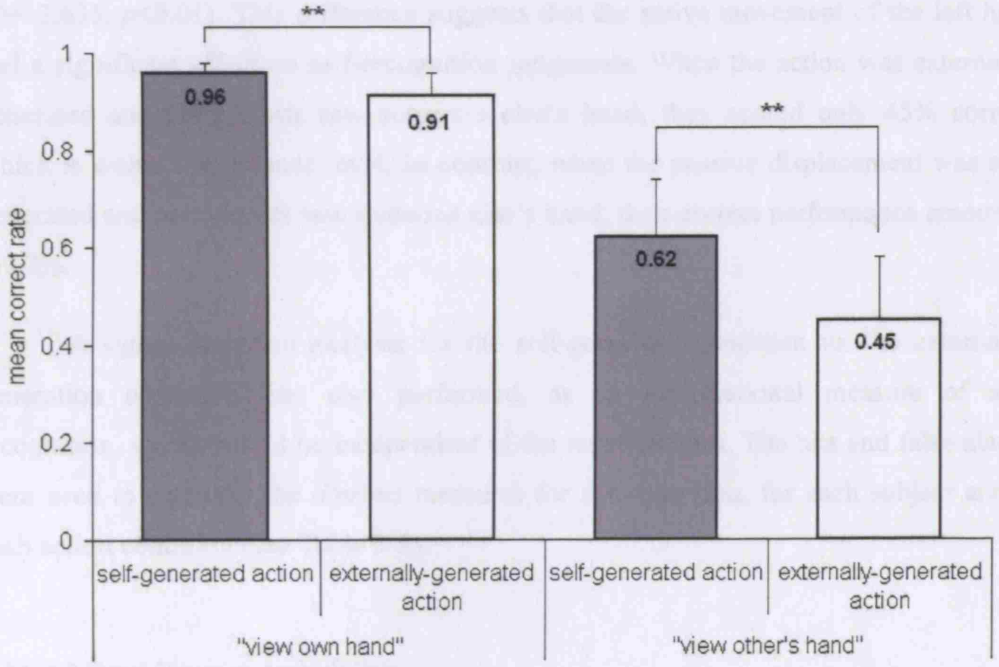

Figure 3-7 Mean correct rates per condition. The error bars represent 95% confidence intervals. Asterisks indicate significant differences in self-recognition between self- and externally-generated movements.

Participants performed almost perfectly in the 'view own hand' condition. This replicates previously reported data (Daprati et al., 1997; Sirigu et al., 1999). In particular, when subjects were looking at their own hand, their correct performance rate was high for both the 'self-generated' and the 'externally-generated' conditions (96% and 91% respectively). Despite this, correct recognition of one's own hand was significantly better when subjects generated the right hand movement themselves, than when the

experimenter generated it (Z=−2.062, p<0.05). This suggests that even when participants saw their own hand, efferent information contributed to a significant degree.

Performance in the 'view other's hand' condition was dramatically worse compared to the 'view own hand' condition, for both the self-generated and externally-generated conditions. This difference reflects a bias to attribute the viewed hand to oneself (see also Sirigu et al., 1999; van den Bos & Jeannerod, 2002). Moreover, the mean correct rates for the 'self-generated action' and the 'externally-generated action' conditions when subjects saw the experimenter's hand were also significantly different (Z=−2.635, p<0.01). This difference suggests that the active movement of the left hand had a significant effect on self-recognition judgments. When the action was externally-generated and participants saw someone else's hand, they scored only 45% correct, which is worse than chance level. In contrast, when the passive displacement was self-generated and participants saw someone else's hand, their correct performance amounted to 62%.

A signal detection analysis for the self-generated condition *vs.* the externally-generation condition was also performed, as an informational measure of self-recognition, which would be independent of the response bias. The hits and false alarms were used to calculate the *d'prime* measures for self-detection, for each subject and in each action condition (see Table 3-2).

Table 3-2 Signal Detection Analysis Data

Condition	**Hits**	**False Alarms**	**Misses**	**Correct Rejections**	***d'prime***
Self-Generated	.96	.38	0.031	.62	3.15
Externally-generated	.91	.55	0.09	.45	1.85

The *d'primes* were submitted to the non-parametric Wilcoxon matched-pairs-tests. Differences between self-generated and externally-generated conditions were significant (Z=2.635, p<0.05), suggesting that participants had access to more discriminative information for self-recognition in the self-generated condition. The mean

d' prime value was 3.15 in the self-generated condition and 1.85 in the externally-generated condition.

Two control experiments that were performed after the main experiment were used to assess the possible influence of confounding factors related to the visual detectabilty and discriminability of efferent information in the stimuli used in the main experiment.

3.3.1. Control experiments 1 and 2: Visual Detectability of Efference

Could the visual stimulus carry other information that is confounded with efference? In particular, if subjects could reliably detect when a viewed movement of the right hand was actively generated by the left hand, and if they also knew on a particular trial that they did not make any active movement of their left hand themselves, it would follow that the visual stimulus showed another person (see condition 4, Figure 3-4). The low accuracy in self-recognition when viewing another person's hand in the externally-generated condition (45% correct) suggests that subjects did not in fact have access to purely visual information about efference. However, this possibility was formally tested in control experiment 1. This control could not be embedded in the main experiment, since the direct instruction to judge efference might well lead subjects to exaggerate or idiosyncratically pattern their active movements in all trials. This strategy would artificially boost the role of efference in self-recognition, thus altering the phenomenon under investigation.

Control Experiment 1

Two actors were used to produce a total of 80 video clips of 2 sec duration, 40 for each actor. The same logic and apparatus as in the main experiment was used. The actors could either press the left side of the lever themselves so as to produce a passive displacement of their right index finger, or the lever could be pressed by someone else. Only the movement of the right hand was filmed. During the making of the movies, the actors did not have direct view of their hand, and they were asked to press with their left index finger the left end of the lever as soon as they heard an auditory tone (go-signal). The length of the movies was the same as in the original experiment (2 s). Half of the clips showed self-generated movements and the other half showed externally-generated movements.

Eighteen new volunteers with normal or corrected to normal vision, all right-handed took part in this experiment (mean age 28, 10 females). Note that the volunteers were viewing the movements made by actors rather than their own movements. This ensured that they judged purely the visual character of the actions that they observed, and could not rely on stored efferent (Knoblich & Flach, 2003) or proprioceptive memories gained when making the movements. Subjects were first trained in visual recognition of the movements by seeing exemplars of how a movement of the right hand could be self-generated or externally-generated. They, then, saw 2 training movies in which both hands of the actors were shown, so that subjects could clearly see whether the movement of the right hand was generated by the actors themselves or by another person. Following the training, subjects viewed movies in which only the passive displacement of the right hand was seen just like in the main experiment. They were asked to judge whether the passive displacement of the right hand shown in each movie was self- or externally-generated. Each subject saw 40 movies, 20 for each condition, in a random order. Half of the subjects saw 40 movies of actor 1, and the other half 40 movies of actor 2.

The mean correct rates were 59% for the self-generated movies and 54% for the externally-generated movies (see Figure 3-8).

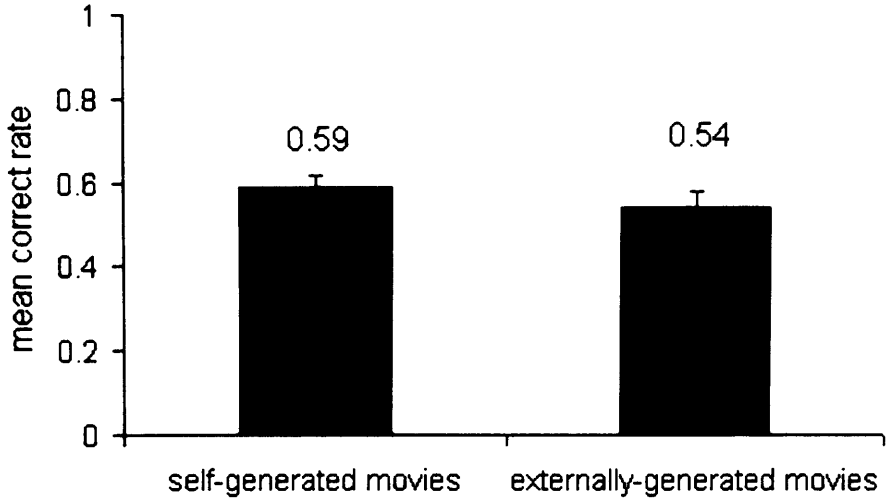

Figure 3-8 Mean correct rates for Control Experiment 1. Errors bars indicate standard errors.

The mean correct rates per subject were submitted to the non-parametric Wilcoxon matched-pairs-tests. Differences in accuracy between the two conditions were not significant (Z=−1.45, p>0.05), suggesting that the visual differences between the

kinematics of a self-generated displacement vs. an externally-generated displacement were minimal. Moreover, this non-significant effect was present even when the data were analyzed according to which actor was used to produce the movies ($Z=-.42$, $p>0.05$ for the movies of Actor 1, and $Z=-1.86$, $p>0.05$ for the movies of Actor 2).

Control experiment 2

The two actors that were used to produce the movies were also tested two weeks later in the same task (control experiment 2). Each actor saw 40 movies of her own hand. In half of the movies, the displacement of the right index finger was self-generated, and in the other half it was externally-generated. The task was to judge whether the passive displacement of the right index finger was self- or externally generated.

Actor A scored 60% correct at detecting self-generated movements and 60% correct at detecting externally-generated movements. Actor B scored 55% correct at detecting self-generated movements, and 50% correct at detecting externally-generated movements. This pattern of results suggests that even the authors of an action did not show enhanced visual classification of these same movements depending on whether they were self- or externally-generated. Due to the small number of participants, no statistical analysis was applied.

Taken together, the results from these 2 control experiments suggest that participants could not have used visual information *alone* to judge whether a movement was self- or externally-generated. In other words, there were no clear differences between self- and externally-generated movements in the visual stimulus that could be used by the participants as a basis for self-recognition judgments in the original experiment. Moreover, the chance level of performance in the "externally-generated/view other's hand" condition (condition 4, see Figure 3-4, and 3-6) of the main experiment suggests that participants did not base their judgments on such information. Therefore, the use of lever was an appropriate method to separate efference from afference, because it minimized the visual differences in the kinematics of the passive displacement between conditions.

3.3.2. Control experiment 3: Visual Discriminability of Efference

A second possible explanation of the result of the main experiment relates to another potential visual difference between conditions. In principle, self-generated movements might carry more visual information than externally-generated movements, for example if subjects deliberately made "exaggerated" or unusual patterns of movement in the self-generated condition. This might involve a motor strategy to produce particular movement patterns that are highly visually identifiable. On this hypothesis, individual exemplars of self-generated movements should have higher visual discriminability than individual exemplars of externally-generated movements. Therefore, a second control experiment was performed to assess the visual discriminabililty of these movements. As with the first control experiment, this experiment could not be embedded within the main self-recognition experiment, because doing so might have introduced motor strategies that would artificially boost the efferent contribution to self-recognition.

Participants watched pairs of movies. The movies were the same as in control experiment 1. Each pair consisted of either (a) two repeats of the same movie in which the passive displacement was self-generated, or (b) two different movies in both of which the passive displacement was self-generated, or (c) two repeats of the same movie in which the passive displacement was externally-generated, or (d) two different movies in both of which the passive displacement was externally-generated (see Table 3-3). If in the self-generated actions, participants used a motor strategy of exaggerating their movements, so that they would be more easily recognizable, then discrimination between movies should be better for the self-generated than for externally-generated movements.

Table 3-3 The stimuli used in Control Experiment 3

	1st Movie	**2nd Movie**
Pair Type 1	Self-generated	**Same** self-generated movie
Pair Type 2	Self-generated	**Different** self-generated movie
Pair Type 3	Externally-generated	**Same** externally-generated
Pair Type 4	Externally-generated	**Different** externally-generated

Eighteen new volunteers with normal or corrected to normal vision, all right-handed (mean age 27, 8 males) took part in the experiment. Each participant watched a total of 80 pairs of movies (20 pairs of movies for each category) in a random order. The

task was to judge whether the two movies in each pair were the same or different. In this control experiment the focus of interest was the visual discriminability of movement exemplars.

When participants watched a repetition of the same movie, they correctly detected the repetition on 66% of trials in the self-generated condition, and 66% in the externally generated condition. When, participants watched a pair consisting of 2 different movies, they correctly discriminated them on 45% of trials in which two self-generated movements were shown, and 46% of trials in which two externally-generated movements were shown. Figure 3-9 shows the mean correct rates across conditions.

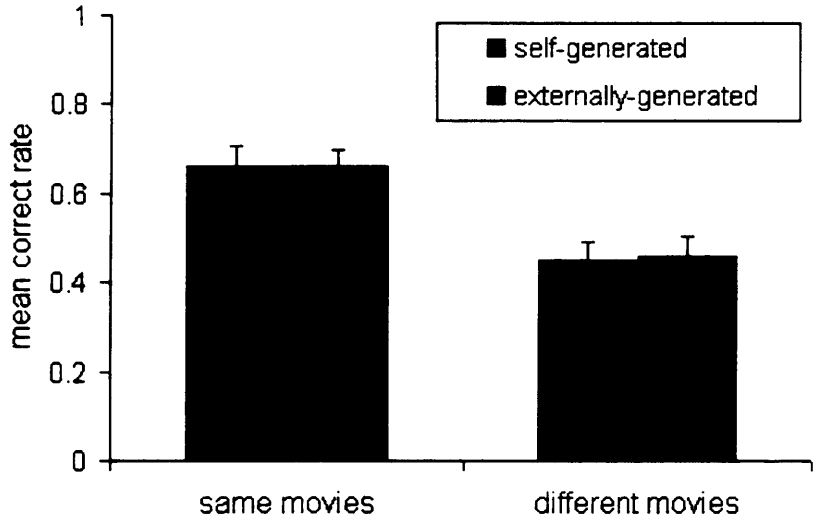

Figure 3-9 Mean correct rates for Control Experiment 3. Error bars indicate standard errors.

A signal detection analysis was used, in which the signal was defined as the detection of a difference between the two movies in a pair. The d' primes were calculated per condition and per subject, and were submitted to the non-parametric Wilcoxon matched-pairs-tests. Differences in performance for detecting visual differences between self-generated and externally-generated movements were not significant ($Z=-.710$, $p>0.4$). Thus, visual discriminability was no higher for self-generated than for externally-generated movements. This suggests that the use of a lever as a means of manipulating efference was successful in minimizing possible visual confounds associated with the presence or absence of efference. The level of visual information was comparable across conditions.

3.4. Discussion

Self-recognition judgments were more accurate when subjects made a voluntary action, even if this action was unseen and spatially remote from the part of the body that had to be recognized. The efferent information clearly contributed to the match between proprioceptive and visual representations that underlies the self-recognition task. Before discussing precisely how efferent information contributed to self-recognition, the role of possible artefactual explanations is discussed.

One possible confounding factor would be the presence of a mean difference in movement latency between the self-generated and externally-generated conditions. However, several features of the design suggest that this did not occur. First, when the experimenter clearly detected a difference between the subject's and the second experimenter's movement, the trial was excluded. Second, the use of a single motor action and an auditory go-signal at fixed 500 ms latency after the image onset were employed to allow rapid reaction times and stereotyped movement patterns. Third, if there were major differences in movement onset times, one would expect that correct rejections when subjects saw the experimenter's hand in the self-generated condition would be as high as hits when they saw their own hand. In fact correct rejections were significantly less frequent than hits (Z=−3.68, p<0.01, see Table 3-2). Finally, significant differences between "self-generated" and "externally-generated" conditions were found even when subjects were looking at their own hand. In this condition, visual and proprioceptive information are *perfectly* synchronised, and therefore there can be no temporal mismatch to detect. In this case, the benefit of efference could not be an artefact due to an increase in the difference in movement onset or movement kinematics between visual and proprioceptive signals. Therefore, the significant differences found between self- and externally-generated conditions reflect a genuine contribution of efferent information *per se*.

Could there be differences in the detailed kinematics of the passive displacement of the right index finger between the self-generated and externally-generated conditions? The thrust of this argument is that self-generated movements might be recognisable through their specific visual form, without the participant needing to use efferent information in the visual-proprioceptive matching process. The first two control experiments compared the information available in the visual stimulus between self-

generated and externally-generated conditions. The results showed that participants could not use visual information alone to judge whether a movement was self-generated or externally-generated. The third control experiment investigated whether the levels of visual information in exemplars of self-generated movements were higher than in exemplars of externally-generated movements, using a visual discrimination task. Discrimination performance did not differ between conditions, suggesting that participants could not have used purely visual information for self-recognition. Both the control experiments involved the participants viewing movements of another person's hand in all the trials. Such control experiments could not be interleaved with the main experiment, because the question asked in the control experiments has a "leading" quality, which would encourage participants to make precisely the exaggerated or idiosyncratic styles of movement that the main experiment sought to avoid. However, there is no reason to suppose that the purely visual detectabilty of efference (control experiments 1 and 2), or the visual discriminability of movements (control experiment 3) would be any higher for judgements performed in real-time vs. offline, or for one's own movement vs. that of others. Indeed, the control experiments with new participants provide a strong way of studying the purely visual component of these movements. The null findings show that visual differences cannot explain the efferent contribution to self-recognition in the main experiment. Therefore, the improved self-recognition performance in the self-generated condition of the main experiment must reflect a specific and genuine contribution of efferent information to the process of visual-proprioceptive matching, rather than a difference in the visual stimuli alone.

Main finding I: Efferent advantage

Previous studies on self-recognition have identified the critical condition as the one in which subjects watch someone else's hand performing the same movement (see conditions 2 and 4 in Figure3-4, see also Daprati et al., 1997 and Sirigu et al., 1999). In the present study, subjects were significantly more accurate in correctly recognizing their own hand when the passive displacement was self-generated compared to when it was externally-generated. In the absence of efferent information, just by comparing visual and proprioceptive signals, subjects were unable to accurately discriminate between self and other, and performed at chance. When the action was externally-generated, subjects incorrectly attributed the experimenter's hand to themselves in 55% of the trials, whereas for the self-generated action incorrect attribution to the self occurred in 38% of the trials.

The difference between these two conditions shows that efferent information makes a specific contribution to self-recognition. Moreover, a novel finding of the present study is that even when subjects were looking at their own hand, their performance was significantly improved when efference was present.

Main finding II: Afferent disadvantage

The observed pattern of results suggests that afferent information is not sufficient for accurate self-recognition. Other studies confirm that proprioceptive information can be over-ridden or altered to produce an anomalous sense of self. For example, during the Rubber Hand Illusion, when tactile stimulation is applied simultaneously on a rubber hand and a real hand, subjects mislocalize the position of their own unseen hand as being closer to the rubber hand that it really is (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005b). During the illusion, participants tend to feel the touch at the locus where they see the rubber hand being touched, rather than on their real hidden hand. Similarly, in the present study, it seems that the phenomenology of a matching between proprioception and visual feedback is strong enough so as to attribute alien body parts to one's self. It is surprising however, that in the absence of efference, normal participants performed so poorly. This poor performance is particularly surprising since many physiological studies have shown that proprioceptive afferent information about passive movement is highly precise, and includes considerable temporal detail (Prochazka, 1999). It is possible though that the brain network responsible for self-recognition does not have access to this level of detailed proprioceptive information.

Main finding III: Direction of misattribution

Another interesting finding is the direction of misattribution. In general, subjects tended to misattribute the experimenter's hand to themselves, and not the opposite. The same pattern has been reported in several studies (Daprati et al., 1997, Sirigu et al., 1999; Van den Bos and Jeannerod, 2002). The explanation put forward is that self-attribution might be a default mode of attribution, when no clear cues for self-recognition are available (Van den Bos & Jeannerod, 2002). Moreover, the direction of this effect can also be explained by the very nature of the experimental task used and by the prevalent role of vision over proprioception. Other studies have shown that synchronous visual and proprioceptive stimulation is a powerful cue for self-attribution (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005b; Tsakiris, Prabhu & Haggard, *in press*). In the Rubber

Hand Illusion discussed above, synchronicity induces a feeling that a rubber hand is one's own, even when there are clear morphological differences between the rubber hand and the subject's hand.

The role of efference

Given that the results showed a clear efferent advantage in self-recognition, participants must have based their self-recognition judgements on detection of very small differences in either the onset latency and/or kinematic pattern between what they do, and what they feel and see. If the timing and kinematic details provided by viewing the participant's hand and the experimenter's hand were exactly identical, no information would be available to support self-recognition. Efferent information then presumably improves detection of such small timing and/or kinematic differences, but how?

One possible explanation would be that efferent information was not used directly, but instead, it provided an indirect benefit by improving the quality of information in either the proprioceptive or visual feedback pathways. This seems unlikely for two reasons. First, one major effect of motor commands on sensory information is to suppress the magnitude of sensations (Blakemore, Frith & Wolpert, 1999; Blakemore, Wolpert, & Frith, 2000; Shergill et al., 2003; Tsakiris & Haggard, 2003). Therefore, the hypothesis that efference might improve proprioceptive representations seems incompatible with the established efferent down-regulation of proprioceptive re-afference. Could efference improve the visual representation by similar means? A recent self-recognition experiment with a deafferented patient (Farrer, Franck, Paillard, & Jeannerod, 2003b) suggests not. Deafferented patient GL could only perform the task by comparing efferent information with visual information. GL detected differences only when the spatial discrepancies between her own movement and the viewed movement were large (>70° angular bias, whereas for normal subjects it was >40°). This suggests that efferent information alone cannot improve the quality of the visual information. Therefore, the hypothesis that efferent signals influence self-recognition indirectly, by altering the processing of proprioceptive or visual information alone, seems unlikely.

Two possible accounts for the role of efferent information in self-recognition are put forward, which are not mutually exclusive. The discussion of these two accounts is based on a simple model of self-recognition, shown in Figure 3-9. The efferent

information available in the self-generated action condition could be directly used in the matching process. For example, efferent information could provide an additional input to the comparison process. The efferent signal could either be a "raw" motor command (Pathway 1 in Figure 3-10), or could be situated after the motor command has been processed by the forward predictive model (Pathway 2 in Figure 3-10).

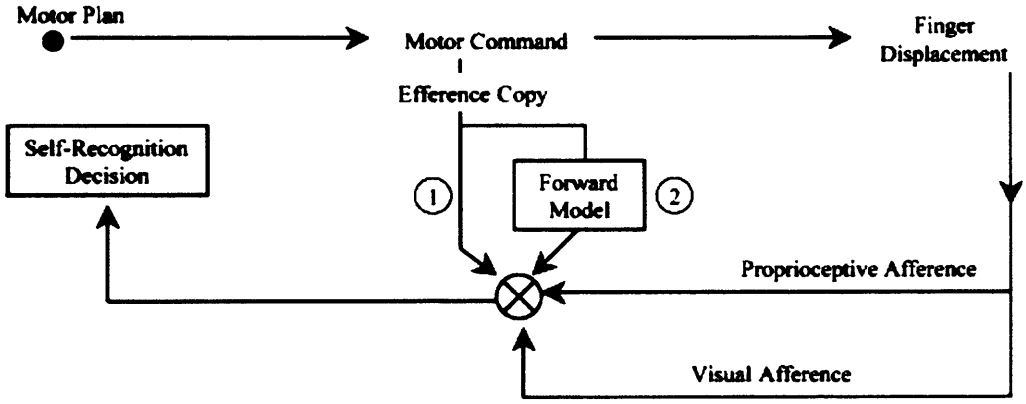

Figure 3-10 A cognitive architecture for self-recognition

A raw efferent copy (Pathway 1) would provide only timing information to the comparator, while a signal processed by the forward model (Pathway 2) could provide a full kinematic description of the movement, suitable for detailed comparison with the proprioceptive or visual signals. The results showed a poor level of self-recognition performance when proprioceptive signals alone were available, and a significant enhancement when efferent signals were used, even when subjects were looking at their own hand. This pattern suggests that the efferent input to the comparator is at least as important as the proprioceptive input. Indeed, the fact that performance was at chance when subjects viewed the experimenter's hand in the externally-generated condition, suggests that proprioceptive inputs to the comparator may be insufficient for correct self-recognition.

The experimental design used in the present study cannot exactly quantify the individual contributions of raw efference and forward model output to self-recognition. However, since the movements were simple finger flexions, pathway 1 may have played

an important role. Comparison between the time of this efferent signal and the time of the passive movement onset may be sufficient for self-recognition. Recently, in a bimanual unloading task, Diedrichsen, Verstynen, Hon, Lehman, and Ivry (2003) showed that efference produces an accurate anticipatory feedforward signal, which enhances the movement representation of the loaded hand. This signal need not detail the full motor parameters of the movement, because the same effect was found when the subjects unloaded the weight with their other hand, but also when they pressed a button that initiated the unloading. The occurrence of a voluntary action appeared to be more important than its precise kinematic form.

Nevertheless, in the present study, efference significantly improved self-recognition even when participants were looking at their own hand. This suggests that the role of efference cannot be strictly limited to the generation of an accurate temporal-signal. When participants were looking at their own hand, proprioceptive and visual signals were precisely synchronous. In this case, an additional efferent temporal signal adds no new information and should not improve self-recognition performance. The fact that performance nevertheless does improve with efference, suggests that efferent information may also contribute via another route, such as the forward model output (Pathway 2 in Fig. 3-9). For example, internal predictive models within the motor system may use efferent information so as to generate a prediction about the anticipated sensory feedback (Wolpert, 1997). This efferent prediction could improve sensory processing, perhaps by enhancing detection of small kinematic differences. Equally, the spatial precision of proprioception can be enhanced by active positioning of the limb (Paillard & Brouchon, 1968). Therefore, over and above the generation of accurate temporal predictions, efference may also provide predictions of current kinematics that improve the detection of kinematic errors. However, in the present experiment, the active movement of the left hand would additionally need to transfer to improved proprioception of the right hand.

The comparator underlying self-recognition judgements may be located in the parietal cortex (Farrer et al., 2003a; Leube, Knoblich, Erb, & Grodd, et al., 2003a; Leube, Knoblich, Erb, & Kircher, 2003b; Sirigu et al., 1999). Previous studies have shown that parietal cortex is an important integration site for multi-modal information including visual and proprioceptive signals (for a review see Graziano & Botvinick,

2002). In addition, recent neuropsychological (Sirigu et al., 2004) and imaging studies (Lau, Rogers, Haggard, & Passingham, 2004) suggest that efferent information is also processed in these same regions. The neural substrates of perception of self-generated movements were also assessed in two recent imaging studies. Farrer et al. (2003a), following the paradigm first reported by Franck et al (2001), introduced spatial distortions (i.e. angular deviations) in the visual feedback of the subject's voluntary movement. Activation in the right inferior parietal lobe was positively correlated with the degree of the spatial distortion. Similarly, Leube and colleagues (2003b) identified a right fronto-parietal network activated when subjects observed a mismatch between the performed movement and the visual feedback.

An anterior–posterior functional differentiation within the parietal cortex for the processing of peripheral and centrally generated signals has been suggested by various research groups (Burbaud, Doegle, Gross, & Bioulac, 1991; Graziano & Botvinick, 2002; Schwoebel, Boronat & Coslett, 2002). The anterior region of parietal cortex forms the somatosensory areas that are responsible for the processing of unimodal and multimodal sensory signals. Posterior parietal cortex has been linked to the planning of movements (for a review see Cohen & Andersen, 2002) of any body-part (Gemba, Matsuura-Nakao, & Matsuzaki, 2004). One recent review emphasises the role of the parietal cortex in multisensory integration and in the generation of intentions (Andersen, & Buneo, 2002), while other authors emphasise its role in the on-line control of actions (Grea et al., 2002).

The impaired performance of parietal patients in a self-recognition task quite similar to that used here may be explained by an impaired ability to compare on-line the sensory feedback with an internally generated representation of the planned movement (Sirigu et al., 1999). Human neuroimaging studies have consistently showed activation in the parietal cortex linked to the sense of agency (Farrer & Frith, 2002; Lau et al., 2004; Ruby & Decety, 2001). One recent study points to a specific role of parietal cortex for action-recognition. MacDonald and Paus (2003) reported impaired action-recognition performance following rTMS over superior parietal lobule (SPL) only for active, but not for passive movements. According to those authors, SPL is specifically engaged in detecting temporal congruencies between efferent and afferent signals.

The authorship effects observed in the present study are in accordance with previous research on the perception (Tsakiris & Haggard, 2003), recognition (Knoblich & Flach, 2001; and Knoblich et al., 2002) and prediction (Blakemore, Frith, & Wolpert, 1999) of effects of voluntary actions. Knoblich and colleagues have shown that efference provides a significant advantage in the prediction and off-line recognition of self-generated events. In these studies, the action and the effect took place on the same body part. The present study extends this evidence by emphasizing the role of efference in recognizing afferent events that occurred to a different body part from the one that performed the action. This significant contribution of efferent signals provides evidence for an authorship effect on self-recognition. This position contrasts with recent philosophical concepts of the "bodily self", according to which proprioception is a basic form of self-consciousness (Bermúdez, 1998). The present results challenge this view and argue against a dominant role of proprioception in action recognition (cf. Farrer et al., 2003b), suggesting that self-recognition in the presence of only afferent information, and without action, is quite limited.

However, the present study also suggests that afferent information alone may be sufficient for self-attribution of a body-part. The Experiments described in the following Chapter focused on the necessary and sufficient conditions for bodily self-attribution during a purely sensory situation, namely during the Rubber Hand Illusion.

4. Self-attribution and Body-ownership: Functional and Neural Signatures of the Rubber Hand Illusion[3]

In Charles Dickens novel 'Our Mutual Friend', the following scene takes place : Mr Wegg, recent amputee, visits Mr Venus' shop. Mr Venus is a taxidermist, and Mr Wegg, because he just found regular employment, wishes to buy back his own severed leg, which Mr Venus has purchased as part of a 'miscellaneous' lot from the local hospital. This is what Mr Wegg says to Mr Venus :

'I have a prospect of getting on in life and elevating myself by my own independent exertions', says Mr Wegg, feelingly, 'and I shouldn't, like I tell you openly I should not like - under such circumstances, to be what I call dispersed, a part of me here, and a part of me there, but should wish to collect myself like a genteel person'.

4.1. Manipulating body-ownership with the Rubber Hand Illusion

When I decide to write, I do not need to look for my hand, in the same way that I have to look for a pen or a piece of paper, for the simple reason that my hand is always present, with *me*. This example illustrates the immediacy of the experience of one's own body. The feeling that the body I inhabit is mine and always with me is called body-ownership. The processes by which the body is experienced as part of the self are far from being fully understood. Though immediate, the bodily experiences are paradoxically also in the background of mental life, and they only become vivid in special circumstances such as pathology.

Several clinical conditions involve abnormal body experiences, such as phantom limb (Ramachandran, 1998), somatoparaphrenia (Bottini et al., 2002), and supernumerary limbs (McGonigle et al., 2002) to name a few (for a review see Haggard & Wolpert, 2005). These conditions show that the 'body always there' in mental life may in fact be a specific cognitive construct, which can be altered when its neural substrates are damaged. The symptoms can be extremely disturbing to the patient, and challenge the normal assumption of a coherent experience of a unitary embodied self.

[3] Experiments 4.1 and 4.2 were published in Tsakiris M & Haggard P (2005a). The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance* **31**(1):80-91. Experiment 4.3 was conducted in collaboration with Maike Hesse, Christian Boy, Gereon Fink and Patrick Haggard.

The brain contains multiple representations of the body that differ in their origin, their function, their neural underpinnings and their phenomenal content (for a review see section 1.4). Primary sources of body-awareness include multisensory signals (e.g. touch, vision, proprioception, interoception), and movement-related signals (e.g. efference copy and computations of the motor system). These primary signals are modulated by cognitive representations of the "body in the brain" (e.g. body schema and body image). But how does the sense of body-ownership arise in the brain? It is particularly difficult to study the neural and functional signatures of body-ownership experimentally, simply because the body is "always there" (James, 1890/1981). It would be therefore particularly difficult to design an experiment where the sense of body-ownership could be isolated, by direct manipulations making it present in one experimental condition and absent in another.

The Rubber Hand Illusion (RHI) provides a viable way of experimentally investigating body-ownership, because it allows for an object to be linked to the body, or not, under experimental control. Watching a rubber hand being stroked synchronously with one's own unseen hand causes the rubber hand to be attributed to one's own body, to "feel like it's my hand" (Botvinick & Cohen, 1998). Attribution can be measured quantitatively as a drift of the perceived position of one's own hand towards the rubber hand. A convenient quantitative proxy of the RHI is the tendency to believe that the position of one's own hand in the external space is actually at the location of the rubber hand. That is, as the rubber hand is incorporated, there is a corresponding tendency for the visually perceived position of the rubber hand to "capture" the proprioceptively perceived position of one's own hand. In one study, after 30 minutes of synchronous stimulation on the rubber hand and the participant's hand, participants mislocated the perceived position of their own hand (Botvinick & Cohen, 1998). They judged the position of their hand to be closer to the rubber hand, as if their hand drifted towards it.

Botvinick and Cohen suggested that the Rubber Hand Illusion (RHI) reflects a three-way interaction between vision, touch and proprioception: vision captures touch, resulting in a mislocalisation of the tactile percept towards the spatial location of the visually perceived rubber hand. This visual-tactile correlation influences the felt position of one's own hand. At the phenomenological level, the illusory experience seems like a form of incorporation of a foreign object, as if the rubber hand becomes a "bodily

auxiliary" (Merleau-Ponty, 1962). The end result of the RHI, namely a visual adaptation of proprioceptive position, is somewhat similar to prism adaptation (Welch et al., 1979). However, the key feature of the RHI is that it results from correlated visual and tactile inputs. This interplay between vision and touch has been at the centre of research on multisensory integration (for a review see Maravita, Spence & Driver, 2003). It has been consistently shown that vision usually plays a dominant role over touch and proprioception (Ernst & Banks, 2002). For example, even non-informative vision of body parts exerts a top-down influence on tactile percepts by improving the spatial resolution of touch (Haggard, Taylor-Clarke & Kennett, 2003; Kennett, Taylor-Clarke & Haggard, 2001).

Importantly, the RHI can be used as a method of investigating not only multisensory integration and the interplay between vision, touch, and proprioception, but also the way the bodily self is constituted, integrated and perceived by the brain.

Is the bodily self the construct of statistical correlations?

The initial experiment by Botvinick and Cohen (1998) suggests that the necessary condition for the inducement of the Rubber Hand Illusion is the presence of synchronized visual and tactile stimulation. Another experiment by Armel and Ramachandran (2003), using a slightly different paradigm, extends this view by suggesting that visuo-tactile correlation is both necessary and sufficient condition for the RHI. Armel and Ramachandran stimulated the subject's hand and the rubber hand synchronously or asynchronously. After the stimulation period, the experimenter "injured' the rubber hand (e.g. the experimenter bent one of the rubber fingers backwards), and Skin Conductance Responses (SCRs) were measured from the subject's unstimulated hand. As predicted, SCRs were significantly higher after synchronous than after asynchronous stimulation. Consequently, the experimenters investigated whether similar effects would occur when they stimulated (i) a rubber hand that was located in a spatially remote position, and (ii) an external object, in that case a table. As before, after the stimulation, the rubber hand or the table were "injured". Interestingly, SCRs were again significantly higher after synchronous than after asynchronous stimulation in both these visual conditions (see also Ramachandran & Hirstein, 1998). According to the authors this pattern of results suggests that both the fake hand and the table, and in

principle any other object, can be self-attributed, provided that strong visuo-tactile correlations are present.

On the basis of this evidence, Armel and Ramachandran concluded that this illusion ("it feels like the fake hand/table is my hand", p.1504) is the result of Bayesian perceptual learning. That would suggest that the RHI is the result of a purely bottom-up mechanism, which associates synchronous visuo-tactile events. In the strong version of this model, any object can become part of "me", simply because strong statistical correlations between different sensory modalities are both necessary and sufficient conditions for self-attribution. The possibility that the background, coherent, bodily self may in fact be built up by prior, repeated, bottom-up multisensory correlations cannot be excluded. Developmental studies suggest that intermodal matching is a prerequisite for self-identification (Rochat & Striano, 2000).

This view is not universal, however. Still, it is an empirical question whether current multisensory experience is assimilated to some representation, a form of "bodily self-consciousness", possibly arising from prior experience or from cognitive body-representations. The literature on body-representation suggests that the body is a unique perceptual object, and thus, body-related percepts are not simply correlated, but they are integrated against a set of background conditions that preserve the coherence of the bodily experience. On this latter view, intermodal matching may not be sufficient for self-attribution. Contrary to the account according to which concurrent visual and tactile stimulation constructs a changed body scheme (Armel & Ramachandran, 2003), it has been suggested that the concurrent visuo-tactile inputs are integrated within a pre-existing representation of one's own body. Neurophysiological studies on monkeys support this view. Graziano and colleagues (Graziano, Cooke, Taylor, 2000) showed that bimodal neurons in parietal area 5 of the monkey brain were sensitive to the position of the fake arm when fake and real hands were stroked synchronously, but only when the fake arm was aligned with the monkey's body. Thus, it seems that these bimodal neurons do not simply integrate visual and tactile percepts, but they integrate them while preserving a coherent representation of the body. In fact, the results by Graziano, Cooke and Taylor (2000) suggest that representations, at least in area 5, may even be detailed enough to incorporate visual discrimination between a left or right hand (see also Maravita, Spence & Driver, 2003).

Introspective evidence from the original experiment (Botvinick & Cohen, 1998) suggested that participants felt not only as if they were feeling the touch at the location where the rubber hand was seen to be touched but also as if the rubber hand was their own hand. In a sense, their tactile sensations were projected onto the rubber hand, which eventually felt like part of their own body. These observations might reflect the involvement of two separate components. First, there is a bottom-up process of integrating synchronized visual and tactile percepts, which is a necessary condition for producing the RHI. Second, this process produces persistent, vivid phenomenological changes in body representation, namely, the experience that the rubber hand is part of one's own body. Moreover, the content of the changed body representation might be quite different from, and goes beyond, the perception of correlated visual and tactile stimulation.

These observations suggest that the RHI could involve an interaction between general body scheme representations and localized visuo-tactile integration. Two issues are in need of clarification. First, how do correlated visual and tactile stimuli come to influence the perceived position of the hand? Second, why and how do correlated visual and tactile stimuli produce this strange phenomenal experience of ownership? Precisely because the RHI paradigm allows for the manipulation of body-ownership, it is an appropriate method for the study of the necessary and sufficient conditions for bodily-self-attribution. The experiments described in this Chapter aimed at highlighting the influence of top-down and bottom-up processes in self-attribution, and the neural and functional correlates of the RHI.

4.2. Re-visiting the Rubber Hand Illusion: visuo-tactile integration and body scheme representations

Experiments 4.1 and 4.2 investigated the modulation exerted by general body scheme representations on the RHI. In experiment 4.1, the main experimental manipulation involved (a) the posture of the viewed rubber hand and (b) the identity of the viewed object, and in experiment 4.2, the main experimental manipulation involved the hand-identity of the viewed rubber hand.

4.2.2. Experiment 4.1

4.2.2.1. Experimental Design & Methods

Design

Experiment 4-1 investigated the influence of the viewed stimulus content on the RHI, by manipulating:

(a) the body configuration, and

(b) the identity of the viewed object.

This experiment was informed by previous suggestions in the literature. For example, Pavani, Spence and Driver (2000) showed that the interference effects of viewing rubber hands, while participants were tapped on their own hands, were operative only when the posture of the rubber hand was congruent with the participant's own posture. In that study, participants had to discriminate vibrotactile stimuli delivered either at the index or the thumb of their own unseen hand, while they were looking at a rubber hand "holding" distractor lights. The effect of the distractor lights was increased only when the rubber hand was in a congruent position with respect to the subject's hand, and decreased when the rubber hand was in an incongruent position.

Similarly, in the present study, the posture of the rubber hand was manipulated. Participants watched a rubber hand in a congruent position with their own hand (0°), or a rubber hand in an incongruent position, rotated by -90° with respect to their own hand. In a further condition, the rubber hand was replaced by a neutral object. Viewing a neutral object was included to clarify whether the RHI is caused by a purely bottom-up association of visual and tactile events (see Armel & Ramachandran, 2003;

Ramachandran & Hirstein, 1998), and thus it is not specific to body-parts. If the RHI is caused by the mere correlation of visual and tactile percepts, then any visual stimulus will induce a similar illusion, provided that the visuo-tactile correlation between the object and the participant's hand is appropriately correlated. Therefore, in that condition, the rubber hand was replaced by a wooden stick.

For the RHI to occur, visual and tactile percepts should be temporally synchronized (Botvinick & Cohen, 1998). A repeated-measures design was used, in which an experimental condition of synchronous stimulation between the viewed object and the rubber hand was compared to a control condition of asynchronous stimulation. In previous studies (Botvinick & Cohen, 1998), the mode of stroking was a between-subjects factor, whereas in the present study it was a within-subjects factor.

To recap, the experimental factors were: (i) the viewed object (rubber hand at 0°, rubber hand at -90°, wooden stick), and (ii) the mode of stroking (synchronous vs. asynchronous). The conditions were blocked, and each participant performed the conditions in a different random order. Figure 4-1 shows the experimental set-up.

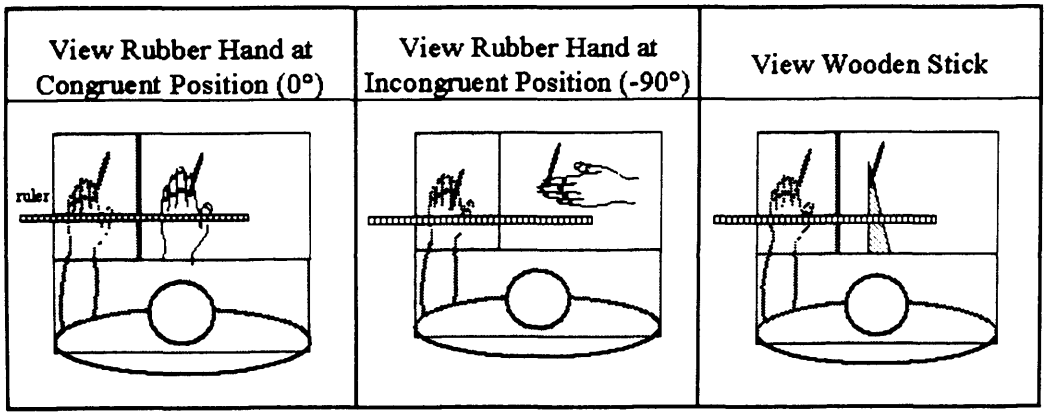

Figure 4-1. Experimental set-up in Experiment 4.1. Participants saw in different conditions (a) a rubber hand in a congruent posture, (b) a rubber hand in an incongruent posture, or (c) a wooden stick. The participant's left hand was out of sight for the whole duration of the experiment. The rubber hand or the wooden stick appeared, aligned with the subject's midline, only during the stimulation and disappeared during the judgment period. Participants judged the perceived position of their finger by indicating a number on a ruler presented in front of them (see text for details).

Methods

Participants sat in front of a table. At the beginning of each block, their left hand was placed by the experimenter at a fixed point inside a frame, whose top-side was covered by one-way and two-way mirrors. The two-way mirror was used to make the rubber hand appear (during stimulation) and disappear (during judgment). At the beginning of each block, both the subject's left hand and the rubber hand were out of sight. A pre-test baseline estimate of finger position was obtained prior to stimulation. Subjects saw a ruler reflected on the mirror. The ruler was positioned 18cm above the mirror, so as to appear at the same gaze depth as the rubber hand. Participants were asked: "Where is your index finger?", and verbally reported a number on the ruler in response. They were instructed to judge the position of their finger by projecting a parasagittal line from the centre of their fingertip to the ruler. During the judgments, there was no tactile stimulation, and the lights under the two-way mirror were switched off, to make the rubber hand/stick invisible, leaving only the ruler visible.

After the judgment, the ruler was removed, and the lights under the two-way mirror were turned on, to make the rubber hand (or stick) appear. The participants were viewing the rubber hand (or stick) in the same depth plane as their own hand. The distance between the real hand and the viewed object was 17.5 cm. Stimulation was delivered manually by the experimenter with the use of two identical paintbrushes, over 4 minutes. Participants were always stimulated horizontally on the index finger of their left hand, and the rubber hand was stimulated on the index finger in the same way. Both the participant's hand and the rubber hand wore identical rubber gloves, to eliminate visual, tactile and auditory differences. The tip of the wooden stick was also covered with the same elastic material for the same reasons. In the synchronous conditions, both the participant's hand and the viewed object were stroked simultaneously and at the same location. Stimulation was delivered manually along the index finger from the knuckle to the fingertip. Each stroke lasted approximately 500ms-1000ms. The experimenter immediately repositioned the brush at the knuckle and began the next stroke some 500-1000 ms after the end of the previous stroke. In the asynchronous conditions, visual stimulation preceded tactile stimulation and the asynchrony was randomly varied between 500-1000ms.

After the stimulation period, the lights were automatically turned off. The ruler was always presented with a random offset to ensure that participants judged finger position anew on each trial, and that they could not simply repeat previous responses. Participants were asked "Where is your index finger?". After their answer the ruler was removed, and they were asked to move their left hand, and have a rest for a few moments. Following the rest period, their left hand was again passively placed at a pre-determined point, under the frame, and out of sight. The same process was followed for each condition.

Participants

Eight volunteers (mean age 26.7, 4 female), all right-handed, with normal or corrected to normal vision participated in this study, after giving their informed consent. Subjects were naïve as to the purpose of the experiment, and had no prior knowledge or experience of the RHI. The procedures were approved by the local ethical committee.

4.2.2.2. Results

A baseline pre-test judgment was obtained prior to stimulation and a post-test judgment after stimulation. The pre-test judgment errors were subtracted from the post-test judgment errors prior to analysis. Figure 4-2 therefore shows the change in the perceived position of the hand between the start and end of the stimulation period, across conditions. The term "proprioceptive drift" is used to refer to this quantity. A positive drift represents a mislocalisation towards the viewed object (rubber hand/wooden stick). This change in the proprioceptively perceived position of the subject's hand due to stimulation is the main dependent variable.

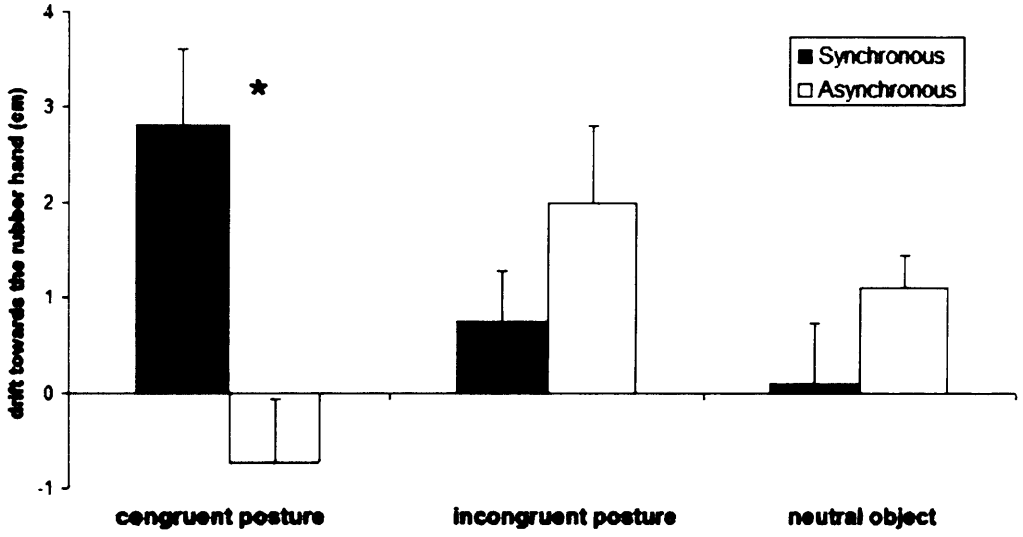

Figure 4-2 Mean proprioceptive drifts towards the rubber hand in Experiment 4.1. Error bars indicate standard errors. Asterisk indicates significant differences between synchronous and asynchronous stimulation. Point "zero" represents the felt position of the participant's hand prior to stimulation.

First, a 2x3 ANOVA was performed on the proprioceptive drifts with two within-subjects factors. The factors were (a) the mode of stroking (synchronous vs. asynchronous), and (b) the viewed object (rubber at 0°, rubber at -90°, wooden stick). None of the main effects were significant ($F(1,7)=0.76$, $p>0.05$ for the mode of stroking, and $F(2,14)=0.59$, $p>0.05$ for the viewed object). The interaction of the two factors was significant ($F(2,14)=7.96$, $p<0.05$). To investigate this interaction further, Simple

Effects Analysis (Howell, 1977) was used to compare the proprioceptive drift between synchronous and asynchronous conditions, for each visual stimulus condition.

Differences between synchronous/asynchronous conditions were significant only when participants saw a rubber hand at a congruent posture with their own hand ($t(7)=4.25$, $p<0.006$, 2-tailed). Differences between synchronous/asynchronous conditions when looking at a rubber hand in an incongruent posture ($t(7)=-1.1$, $p>0.05$, 2-tailed) , or when looking at a wooden stick ($t(7)=-2.04$ ($p>0.05$, 2-tailed) were not significant. Indeed, in these last two cases the drifts for the asynchronous condition were larger than the drifts for the synchronous one, contrary to prediction.

Inspection of Figure 4-2 shows a particularly strong drift of the felt position of the hand towards the rubber hand following synchronous stimulation, especially when subjects viewed a rubber hand in a "congruent posture". However, some drift is seen even after asynchronous stroking for the "incongruent posture" and "stick" conditions. This suggests that drift towards the viewed object may reflect a non-specific effect of visual or tactile stimulation on proprioceptive representation, or may occur due to other factors also. For example, even during the pre-test judgments, participants perceived their finger to be closer to the midline than it really was. This effect might reflect the reported bias in perceiving the position of the hand as closer to the midline than it truly is (Ghilardi, Gordon & Ghez, 1995).

The main focus here is on the change on the felt position of the participant's hand due to visual-tactile integration. This component can be defined as the additional change in positional drift when visual and tactile stimuli are correlated (i.e. synchronous conditions), over and above the drift caused by the same stimuli when they are less clearly correlated (i.e. asynchronous conditions). Therefore, to obtain a more specific measure of the RHI, the proprioceptive drifts obtained in the asynchronous conditions were subtracted from the proprioceptive drifts obtained in the synchronous conditions. The term "perceptual shifts" refers to this quantity. The perceptual shift measure was positive when subjects viewed a congruent hand posture (+3.56cm), but was negative when subjects viewed an incongruent posture (-1.13) or a neutral object (-1.18).

Two planned comparisons were performed on the perceptual shifts. First, the perceptual shifts for "View Rubber Hand at Congruent Posture" were compared to the

perceptual shifts for the "View Rubber Hand at Incongruent Posture". The difference was significant ($t(7) = 2.9$, $p<0.02$, 2-tailed) suggesting that for the RHI to occur, the rubber hand had to be in a congruent position with respect to the participant's hand. Second, the perceptual shifts for "View Rubber Hand at Congruent Posture" were compared to the perceptual shifts for "View Wooden Stick". The difference was significant ($t(7)=4.3$, $p<0.004$, 2-tailed), suggesting that simple association of synchronous visuo-tactile events between the participants hand and the neutral viewed object did not suffice to induce large proprioceptive drifts. In fact, the perceptual shifts for the "view wooden stick" conditions were not significantly different from zero ($t(7)=-2.04$, $p>0.05$).

Overall, the results of Experiment 4.1 suggest that the RHI occurs only when the viewed rubber hand is in congruent posture with the subject's unseen hand. Moreover, the mere correlation of tactile and visual stimulation between one's own hand and a neutral object, such as a wooden stick, does not suffice for eliciting the RHI.

4.2.3. Experiment 4.2

4.2.3.1. Experimental Design & Methods

Design

Experiment 4.2 investigated the relative importance of the two components of the RHI, namely, the influence of a general body scheme representation and the process of visual-tactile integration. To investigate the general top-down effect of body representation on the RHI, the handedness identity of the viewed rubber hand was manipulated. Judgments of hand laterality are particular relevant to body-representation (Schwoebel & Coslett, 2005). The specific question addressed in Experiment 4.2 was whether the RHI would be present if participants were stimulated on their left hand, while they were watching a right rubber hand being stimulated synchronously and at the same location.

Participants were always stimulated on their left middle finger, and they saw a left or a right rubber hand being stimulated on its middle finger. The experimental factors were:

(i) the mode of stroking (synchronous vs. asynchronous),

(ii) whether subjects saw a left or a right rubber hand (congruent vs. incongruent hand identity), and

(iii) the finger judged (middle vs. thumb).

Since the relative position of the middle finger is the same for both left and right hands, we stroked the knuckle of the middle finger in all conditions. The position of the thumb is symmetrically opposite between left and right hands. Therefore, judgments of the perceived position of the thumb might be especially sensitive to whether subjects viewed a left or a right rubber hand, in comparison to judgments of middle finger position. We hypothesized that the perceived position of the thumb would be particularly sensitive to whether subjects experienced the RHI while looking at an incongruent rubber hand identity.

There were, therefore, 4 experimental and 4 control conditions. In the experimental conditions, both the rubber hand and the subject's hand were stroked synchronously, whereas in the control conditions the rubber hand and the subject's hand were stroked asynchronously. The conditions were blocked. Each participant performed the blocks in a different random order. The experimental design and the set-up are shown in Figure 4-3.

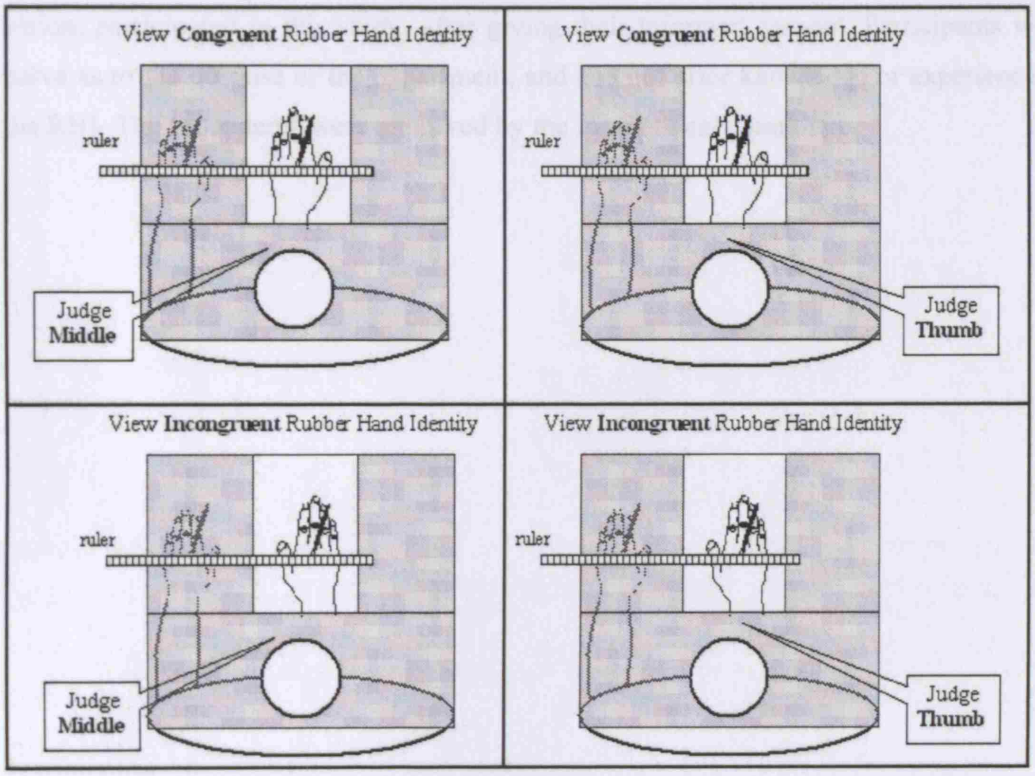

Figure 4-3. Experimental design and set-up in Experiment 4-2

Methods

Stimulation lasted 4 minutes. After the stimulation period, the rubber hand was covered, and a ruler was presented on a horizontal surface, 18cm above their fingertips and aligned with the subjects' fronto-parallel plane. Participants were asked: "Where is your middle finger/thumb?", and verbally reported a number on the ruler in response. They were trained to judge the position of their finger by projecting a parasagittal line from the centre of their fingertip to the ruler. They repeated the judgment 4 times, at

15sec intervals. The ruler was always presented with a random offset to ensure that participants judged finger position anew on each trial, and that they could not simply repeat previous responses. Other aspects of the method were the same as in Experiment 4.1.

Participants

Eight volunteers (mean age 24, 8 females), with normal or corrected to normal vision, participated in this study, after giving their informed consent. Participants were naïve as to the purpose of the experiment, and had not prior knowledge or experience of the RHI. The procedures were approved by the local ethical committee.

4.2.3.2. Results

Figure 4-4 shows the mean proprioceptive drifts across conditions, averaged across the 4 post-test trials. The analysis showed that the RHI was stationary over that period of 1 minute. Only very minor differences were found across these 4 estimates, particularly in the synchronous conditions. The range across these 4 estimates was 8mm in the worst case and only 2mm in the best case.

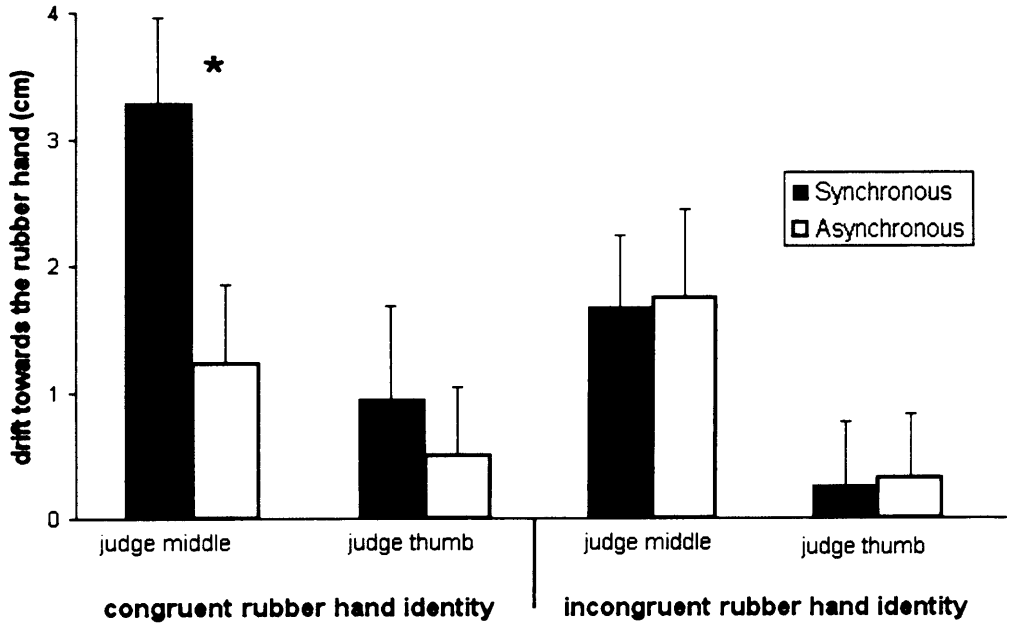

Figure 4-4 Mean proprioceptive drifts towards the rubber hand in Experiment 4.2. Error bars indicate standard errors. Asterisk indicates significant differences between synchronous and asynchronous stimulation.

The proprioceptive drifts across conditions were submitted in a 2x2x2 ANOVA with three within-subjects factors. The factors were (a) the rubber hand identity (congruent vs. incongruent), (b) the finger judged (middle vs. thumb), and (c) the mode of stroking (synchronous vs. asynchronous). There was a significant main effect of the finger judged ($F(1,7)=6.48$, $p<0.05$), and of the mode of stroking ($F(1,7)=6.45$, $p<0.05$. Moreover, the interaction of the three factors was significant ($F(1,7)=10.4$, $p<0.05$).

Simple effects analysis was used to investigate this pattern of interaction in more detail by comparing the synchronous versus asynchronous conditions for each level of the other factors. This showed that differences between synchronous/asynchronous conditions were significant only for judgments of the middle finger position, when participants were looking at a congruent rubber hand ($t(7)=3.89$, $p<0.04$, 2-tailed). Differences between synchronous/asynchronous stimulation for all the other conditions were not significant ($t(7)=.736$ $p>0.05$ when judging thumb/looking at congruent rubber hand, $t(7)=-.279$, $p>0.05$ when judging thumb/looking at incongruent rubber hand, and $t(7)=-.159$, $p>0.05$when judging middle/looking at incongruent rubber hand). Therefore, significant proprioceptive drifts occurred only when participants watched a congruent rubber hand (i.e. left), and judged the position of the stimulated finger (i.e. middle).

To isolate the part of the positional drift due to visual-tactile integration, and obtain a true measure of RHI, the mean perceptual shifts were calculated as before (see Experiment 4.1): the proprioceptive drifts obtained in the asynchronous conditions were subtracted from the proprioceptive drifts obtained in the synchronous conditions. The resulting perceptual shifts were investigated using 2 planned comparisons.

The first planned comparison assessed whether the RHI occurs only when seen and felt hand identities are congruent. The mean perceptual shifts for the middle finger, when subjects watched a congruent rubber hand were compared to the mean perceptual shifts for the middle finger when subjects watched an incongruent rubber hand. The difference was significant ($t(7)=2.9$, $p<0.03$, 2-tailed), suggesting that the RHI occurred only when felt and seen hand-identities were congruent. Since an incongruent rubber hand identity did not even induce the RHI, the original prediction regarding the sensitivity of the thumb position was not confirmed. Judgments regarding the thumb position showed only minimal effects, and did not suggest that the RHI occur.

Nevertheless, a second comparison assessed whether the proprioceptive drift is generalized across the whole hand, or whether it is restricted to the locus of stimulation. The perceptual shifts for the stimulated middle finger were compared to those for the unstimulated thumb, when participants were looking at a congruent rubber hand. The difference was significant ($t(7)=3.32$, $p<0.02$, 2-tailed), suggesting that only the stimulated finger was affected by the RHI.

Overall, the results of Experiment 4.2 replicated the findings of Experiment 4.1, regarding the influence of general body-scheme representations on the RHI, since incongruent rubber hand identity, as was the case with the incongruent posture (Experiment 4.1), did not elicit the illusion. Furthermore, the analysis of Experiment 4.2 suggested that there is a localized effect in the induced proprioceptive drift, since large shifts were observed only for the stimulated finger (see Chapter 5).

4.2.4. Discussion

The Rubber Hand Illusion was originally reported by Botvinick and Cohen (1998). When subjects viewed a rubber hand being stimulated in synchrony with their own unseen hand, they reported a feeling that the rubber hand was their own hand, and they mis-perceived the position of their hand as being closer to the rubber hand than it really was. The results reported in the present thesis replicate the illusion originally reported by Botvinick and Cohen (1998) and they are compatible with previous research on crossmodal integration in the RHI (Farné et al., 2000; Rorden et al., 1999). Moreover, they extend our understanding of the RHI by clarifying the respective contributions of bottom-up and top-down influences in the inducement of the illusion.

In experiments 4.1 and 4.2, the main focus was on the role of body scheme representations on the RHI. The results suggested that the RHI occurred only when the rubber hand was in congruent posture or of a congruent identity with respect to the participant's hand. Incongruent rubber hand posture, incongruent rubber hand identity and neutral objects did not elicit similar proprioceptive drifts. These findings implied that mere correlation between visual and tactile percepts is not sufficient for self-attribution. In addition, this measure of the RHI, namely the proprioceptive drift, was limited to the stimulated finger. This point is investigated in detail in Chapter 5.

There are several important methodological differences between the original experiment by Botvinick and Cohen (1998) and the experiments reported in the present thesis. First, in the original experiment, synchronous/asynchronous stimulation was a between-subjects factor, whereas here it was a within-subjects factor. Asynchronous stimulation served as baseline, providing a better control for the effects of physical stimulation. Second, Botvinick and Cohen asked the participants to make inter-manual reaches with their unstimulated hand to the felt position of the index finger of their stimulated hand. In the present experiments, subjects judged the position of their fingers by indicating a number on a ruler presented in front of them, and both their hands were kept still during judgment. In previous experiments (Armel & Ramachandran, 2003; Botvinick & Cohen, 1998), the rubber hand was positioned next to the participant's stimulated left hand. In the present studies, the rubber hand was aligned with the participants' midline. In addition, Botvinick and Cohen stimulated the hands using a

random pattern of movements "distal to the wrist, (on) the dorsal aspect of hand and fingers, including thumb, and fingertips" (Botvinick, personal communication, 2002). Here, the hands were stroked only along the fingers, from the knuckle to the fingertip, and one finger per condition was stimulated.

The results of experiments 4.1 and 4.2 reported in the present thesis challenge the view that intermodal matching is both a necessary and sufficient condition for self-attribution. The results suggest that self-attribution requires a plausible and congruent visual object (i.e. a rubber hand) to bind with a body part. The binding should also respect the general body configuration (i.e. posture, hand identity). That would imply that the visuo-tactile correlation does not create a new *changed* body schema, as suggested by Armel & Ramachandran (2003). Instead, the visuo-tactile correlation is assimilated to an anatomical and congruent body-template that is underpinned by general body-scheme representations. In particular, the RHI occurred only when participants viewed a congruent rubber hand that was stimulated synchronously with their own hand. In these conditions, participants perceived their hand to be closer to the rubber hand than it really was. The RHI did not occur when participants saw: (a) a neutral object, (b) a rubber hand in an incongruent posture, or (c) a rubber hand of an incongruent identity.

On these grounds, the suggestion that the illusion is the product of a purely bottom-up process should be ruled out. Not only does the viewed object need to be a body-part, but it also has to be of congruent identity and in a congruent posture. Even when participants were looking at a rubber hand, the synchronicity of visual and tactile evens did not suffice to induce the RHI. Postural and laterality congruence between the rubber hand and the subjects' own hand seems to be necessary for the inducement of the RHI. Note that these are both background factors which are quite distinct from visuo-tactile stimulation. Therefore, hand posture and hand identity can be identified as two kinds of body representations that modulate the visuo-tactile integration underlying the RHI.

The involvement of top-down factors does not remove the important bottom-up component or the stimulus-driven element of the RHI. As in previous studies, the present experiments showed the necessity of bottom-up processes of multisensory integration for the inducement of the RHI. Only synchronous visual and tactile stimulation resulted in self-attribution of the rubber hand. Further evidence for the influence of the bottom-up

processes was provided by the pattern of proprioceptive shifts. In experiment 4.2, only the finger stimulated was perceived to be closer to the rubber hand than it really was. That is, proprioceptive drifts associated with the RHI were local to the stimulated finger (i.e. the middle finger). It might be argued that the pattern of localized proprioceptive drifts provides support for a bottom-up model of the RHI, because stronger statistical correlations are expected only for the stimulated finger (see Chapter 5). Nevertheless, the results of experiment 4.2 provide only partial support for the Bayesian account of localized proprioceptive drifts. This strong trend for localized drifts was restricted in the case where the stimulated middle finger did not drift when subjects were looking at an incongruent rubber hand identity. In that condition, any tendency to visually capture the tactile stimulation on the subject's middle finger due to strong visuo-tactile correlations was constrained by the presence of an incongruency at the level of a general body scheme representation, namely the hand identity. This paradigm illustrates that the self-attribution of the rubber hand is neither a purely bottom-up effect, nor a purely top-down modulation. Both components are clearly involved.

The results from the two experiments reported here suggest that self-attribution, and hence ownership of the rubber hand, involves the interplay between bottom-up and top-down processes. First, the correlation of sensory inputs in time (i.e. synchronicity) is the main driver of the RHI. Second, the extensibility and adaptation of body representation depend on coherence with pre-existing visual (experiments 4.1 and 4.2) and proprioceptive (experiments 4.1) body representations. Thus, intermodal matching is a necessary, but not a sufficient condition for self-attribution of a rubber hand These results support the view that the process of bodily synthesis and self-attribution arises as an *interaction* between bottom-up processes of multisensory stimulation and top-down influences originating from body scheme representations. Experiment 4.3 aimed at investigating the neural correlates of this interaction and of body-ownership

4.3. Experiment 4.3: Neural Signatures of Body-ownership

4.3.1. Introduction

As already stated it is particularly difficult to design an experiment where the sense of body-ownership could be isolated by direct manipulations, making it present in one experimental condition and absent in another.

One indirect approach that has been used to investigate the neural basis of the relationship between the body and the self is the study of self-attribution of action. Recent neuroimaging experiments have focused on the sense of controlling one's own body (i.e. agency), and have used action-recognition paradigms as a means of investigating the link between the body and the self. In these experiments, the visual feedback of a self-generated hand movement performed by the subject is manipulated by (a) introducing temporal delays (Leube et al., 2003a,b), or (b) angular distortions (Farrer et al., 2003a), or by (c) presenting someone else's hand (Farrer & Frith, 2002). The comparison of the conditions where there is no conflict between the performed and the viewed movement to the conditions with large discrepancies can, in principle, reveal the brain network that is involved in self-attribution of the observed action. This indirect approach has provided valuable results and insights into the possible mechanism of self-attribution or dis-attribution.

Several studies have confirmed the function of a fronto-parietal network that is involved in self-attribution of action. Inferior parietal cortex and insular cortex have been consistently active in such tasks. In a recent study (Farrer et al., 2003a) where subjects were presented with various degrees of distorted visual feedback concerning their own actions, the less the subjects felt in control, the more pronounced the activity was in the right inferior parietal lobe. Conversely, the activity in the right posterior insula was positively correlated with the match between the performed and viewed movement, suggesting that the insular cortex is related to self-attribution. Bilateral activation of the anterior insula was also observed when subjects were requested to attribute an action to themselves compared to a condition where they attributed it to another person (Farrer and Frith, 2002). Leube and colleagues (2003a) showed that when normal participants observed their hand becoming "anarchic" due to an experimental manipulation of the temporal delay of the visual feedback, a right fronto-parietal network (BA44 and

superior parietal cortex) was activated. Another brain area that might be involved in conflict monitoring between one's own intentions and sensory feedback is the dorsolateral prefrontal cortex (DLPFC). Fink et al. (1999) showed that a mismatch between intention, proprioception, and visual feedback specifically activated the right dorsolateral prefrontal cortex.

Importantly, the foregoing studies used action recognition tasks to investigate the sense of controlling one's body (agency) rather than the sense of having or being one's body (ownership). The presence of self-generated movements is necessary for agency, but not for ownership. Voluntary action makes it difficult to isolate the individual contributions of efferent and afferent signals in body representations (see Chapter 3, and Tsakiris et al., 2005). One paradigm that allows us to investigate body-ownership in the absence of movement and efferent information is the Rubber Hand Illusion.

As shown in Experiments 4.1 and 4.2, the Rubber Hand Illusion (RHI) allows for an external object to be treated as part of the body, or not, under experimental control. It is thus one of the few viable designs for investigating body ownership experimentally. In a recent fMRI study, Ehrsson and colleagues (2004) investigated the neural correlates of the RHI. In that experiment, the orientation of the rubber hand was manipulated (i.e. aligned with the participant's own hand or rotated 180°). The timing of stimulation between the participant's hand and the rubber hand was also manipulated (i.e. synchronous vs. asynchronous stimulation of the two hands). Bilateral neural activity in the ventral premotor cortex and frontal operculum reflected the feeling of ownership of the rubber hand, suggesting that multisensory integration of body-related visuo-tactile percepts occurs in the premotor cortex. One limitation of that study was that it focused on the causes (i.e.visuo-tactile integration) of the RHI, namely the process of self-attribution, and not on the neural correlates of the phenomenal effects of the RHI, namely the sense of body-ownership of the rubber hand.

What are the exact functional mechanisms by which the rubber hand is experienced as part of one's own body? The results of Experiments 4.1 and 4.2 presented in this chapter suggest that body-ownership arises by the interaction of bottom-up (i.e. multisensory signals) and top-down (i.e. body scheme representations) processes (see also Tsakiris & Haggard, 2005b).

The present neuroimaging study aimed at specifically investigating the neural correlates of the sense of body-ownership in the RHI. The experimental design used the *interaction* between the bottom-up and top-down factors to investigate the *causes* of the RHI. In addition, this study focused on the correlation between the neural activity and the strength of the RHI as measured by the proprioceptive drift in the felt position of the subject's hand (Tsakiris & Haggard, 2005b). This *correlation* aimed at identifying the neural correlates of the phenomenal *effect* of the RHI, namely the feeling that the rubber hand is part of one's own body. The data were analyzed in two ways. First, the neuroimaging data corresponding to the 2x2 factorial design were analyzed. Second, the neuroimaging findings were correlated to the experience of the illusion as reflected in the behavioural data (i.e. the proprioceptive drift). It was hypothesized that the subtractive design would isolate the brain areas which code the conditions for body awareness (i.e. bottom-up and top-down influences), and the covariate analysis would reveal the neural correlates of the subjective experience of an object being part, or not, of one's own body.

With regards to anatomical localization, it was predicted that the interaction of the two factors would activate premotor and parietal areas (see Ehrsson et al., 2004) when subjects experience the illusion, and prefrontal areas (see Fink et al., 1999) when subjects experience a conflict between what they feel and what they see. Moreover, it was hypothesized that the strength of the illusion as measured behaviourally would be positively correlated with brain areas linked to the sense of self, as those found in previous studies of recognition of one's own action, in particular the insular cortex (Farrer et al., 2003).

4.3.2. Methods

4.3.2.1. Participants

Fifteen naïve healthy right-handed volunteers (mean age 36.8, 9 female) with no history of neurological or psychiatric illness gave their informed written consent to participate in this study. The study was approved by the ethics committee of the University Hospital of the RWTH—Aachen, Germany.

4.3.2.2. Experimental Design

The experimental design was 2x2 factorial. The two factors were: (i) the identity of the rubber hand (congruent to the participant's stimulated hand or incongruent, that is, participants were always stimulated on their right hand, while looking at a left or a right hand, as in Experiment 4.2), and (ii) the mode of stimulation (synchronous stimulation between the rubber hand and the participant's hand, or asynchronous). This design resulted in four conditions which are shown in Figure 4-5.

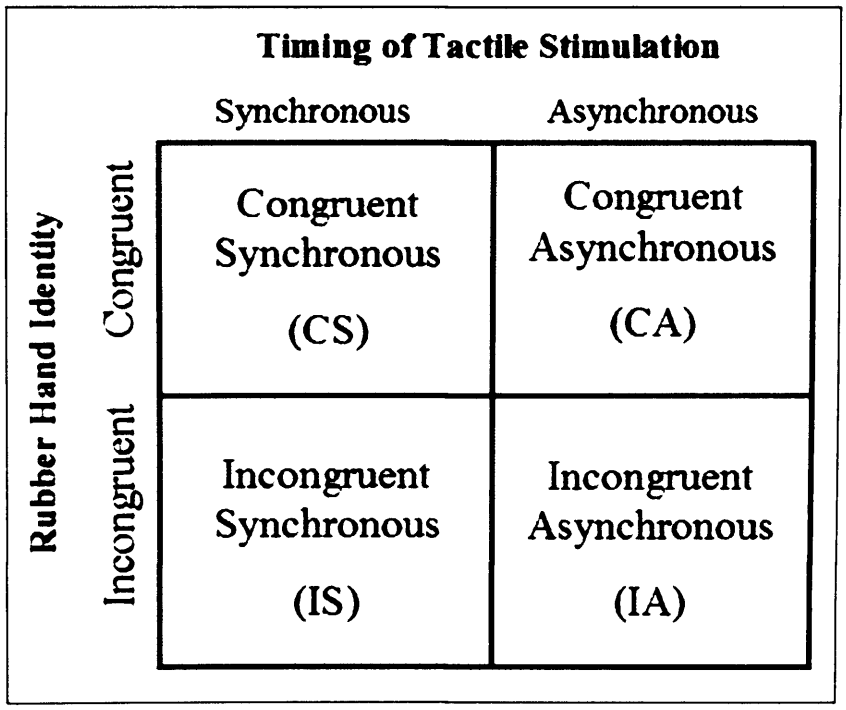

Figure 4-5 Experimental Design of Experiment 4.3

The experiment consisted of 4 blocked conditions, and each condition was repeated 3 times, resulting in 12 trials. Each participant performed the blocks in a different pseudo-random order.

4.3.2.3. Experimental Set-up and Methods

Participants rested in a supine position on the bed in the PET scanner. Their right arm was extended and placed on a tilted support inside a frame. Their right hand was placed by the experimenter at a fixed point inside the frame, whose top-side was covered by a black screen. Participants did not have vision of their hand. The rubber hand was placed on the same frame and was presented in front of the participants, aligned with their midline and on the same plane as their hand. A pair of life-size rubber prosthetic hands was used. The distance between the rubber hand and the participant's hand was 15cm.

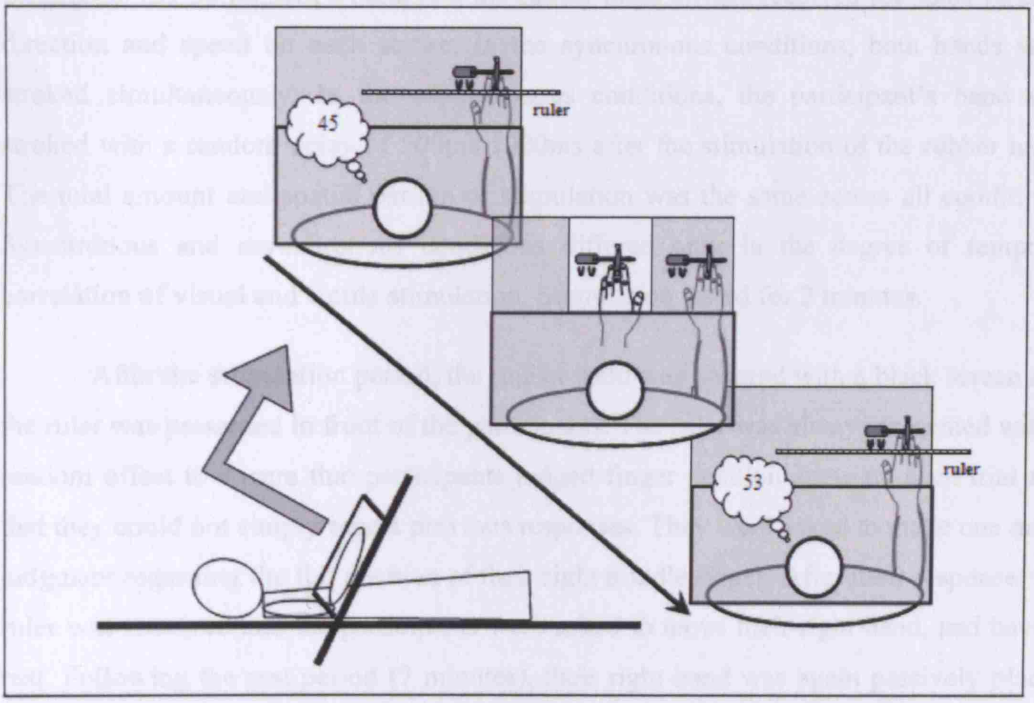

Figure 4-6 Experimental Set-up of Experiment 4.3.

At the beginning of each trial, both the participant's right hand and the rubber hand were out of sight. A pre-test baseline estimate of finger position was obtained prior to stimulation. A ruler was presented on a horizontal surface, 18cm above the hands and aligned with the participant's fronto-parallel plane. Participants were asked: "Where is your middle finger?", and verbally reported a number on the ruler in response. They

were instructed to judge the position of their finger by projecting a parasagittal line from the centre of their fingertip to the ruler. The judgment was recorded and no feedback was given.

After the judgment, the ruler and the black screen covering the rubber hand were removed and tactile stimulation of the hands begun. Stimulation was delivered mechanically by a custom-built stroking machine, consisting of two computer-controlled stepper motors. Participants were always stimulated on the middle finger of their right hand. A left or a right rubber hand was also stimulated on the middle finger. We decided to stimulate the middle finger, because their relative position of the middle finger is the same for both left and right hands. Stimulation was delivered along the middle finger, from the knuckle to the fingertip or vice versa. To simulate the unpredictable nature of manual stroking, the direction and speed of stroking were randomly varied within condition. The participant's hand and the rubber hand always received the same random direction and speed on each stroke. In the synchronous conditions, both hands were stroked simultaneously. In the asynchronous conditions, the participant's hand was stroked with a random delay of 500ms-1000ms after the stimulation of the rubber hand. The total amount and spatial pattern of stimulation was the same across all conditions. Synchronous and asynchronous conditions differed only in the degree of temporal correlation of visual and tactile stimulation. Stimulation lasted for 2 minutes.

After the stimulation period, the rubber hand was covered with a black screen and the ruler was presented in front of the participants. The ruler was always presented with a random offset to ensure that participants judged finger position anew on each trial and that they could not simply repeat previous responses. They were asked to make one more judgment regarding the felt position of their right middle finger. After their response, the ruler was removed and the participants were asked to move their right hand, and have a rest. Following the rest period (7 minutes), their right hand was again passively placed inside the frame, and out of sight. The same procedure was followed for each condition.

At the end of the experiment, participants completed a questionnaire based on a previous questionnaire devised by Botvinick and Cohen (1998). The questions focused on comparing the sense of ownership for each rubber hand identity condition.

4.3.2.4.PET Hardware and Procedures

Measurements of regional cerebral blood flow (rCBF) were taken using an ECAT HR+PET-scanner (CTI-Siemens) and 15O-water using standard technology and procedures previously described in detail (see Weiss et al., 2000 and Weiss et al., 2003). Participants laid comfortably in the PET scanner. An intravenous cannula was placed in their left cubital vein for injection of the radioactive tracer. Each subject underwent 12 PET scans in a single session, comprising three replications of each of the four conditions. Acquisition of the PET data began 45secs after the onset of visuo-tactile stimulation and lasted for 75secs.

4.3.2.5. Imaging processing and statistical analysis

Following standard image preprocessing (including image realignment, image normalization into standard stereotactic space, and smoothing), statistical analyses were performed using SPM2, (http://www.fil.ion.ucl.ac.uk/spm). For each pixel, across all participants and all scans, the mean relative rCBF values were calculated separately for each of the main effects. Comparisons of the means were made using the t statistic and thereafter transformed into normally distributed Z statistics. The resulting set of Z values constituted a statistical parametric map (SPM{Z} map, and thresholded at a Z-score of 3.09 (p<0.001 uncorrected). For the contrasts of interest, the significance of these statistical parametric maps was assessed by comparing the expected and observed distribution of the t statistic under the null hypothesis of no differential activation effect on rCBF.

For all statistical comparisons of interest, the stereotactic coordinates of the pixels of local maximum significant changes in relative rCBF within areas of significant relative rCBF change associated with the specific conditions were determined. Since we were interested in brain activity in the premotor cortex, parietal cortex and right BA44, and we had strong a priori hypotheses, small volume correction (SVC) with a sphere of 10 mm radius was used according to the coordinates of previous studies. To look for other brain activations that were not predicted, we analyzed the SPMs thresholded at p<0.001 (uncorrected) for multiple comparisons at the voxel level or thresholded at p<0.05 (corrected) at the cluster level. Finally, brain activity localization was identified using the atlas of neuroanatomy by Duvernoy (1999).

SPM2 was also used to identify brain areas where activity was associated with the validated quantitative proxy measure of the illusion, namely the proprioceptive drift of the stimulated hand towards the rubber hand (Tsakiris & Haggard, 2005b). To this end, the proprioceptive drift for each trial was used as a covariate and regression with this covariate was calculated for every voxel in the whole brain. The significance of the regression was displayed in a SPM[t] map, which was then transformed into an SPM{Z} and thresholded at $p<0.001$ uncorrected. A small volume correction (SVC) was carried out on the p values of the ensuing maxima on all predicted brain regions. Only those activations that survive whole brain correction at $p<0.05$ or those that survive a SVC at $p<0.05$ (radius 10 mm, corresponding to the spherical region of the posterior insula and the right frontal operculum obtained from the studies of Farrer et al., 2003, and Ehrsson et al, 2003 respectively) are reported.

4.3.3. Results

Fifteen participants took part in this study. One participant was excluded because his head displacement during the experimental session was >6mm.

Unlike previous studies (e.g. Ehrsson et al., 2004), participants were not screened prior to the experiment to check whether they could experience the RHI or not. Because any prior knowledge or experience of the illusion would have confounded the neuroimaging data, we decided to test all the volunteers. Therefore, all participants were naïve as to the purposes of the experiment and did not have any knowledge of the Rubber Hand Illusion. Because we were specifically interested in the experience of the illusion, we included in the analysis only those subjects who experienced the illusion as measured by the proprioceptive drift. We therefore excluded from the analysis 4 participants. In particular, we excluded the participants who did not show larger drifts for the Congruent Rubber Hand Identity condition compared to the Incongruent Rubber Hand Identity (CS-CA) $\leq$ (IS-IA). Since the interaction was taken as our operational definition of sense of ownership (see Experiment 4.2; see also Tsakiris & Haggard, 2005b), the behavioural and neuroimaging data analyzed below refer to the 10 participants who experienced the illusion as measured by proprioceptive drift (6 female, 4 male, mean age 37.2±7.2).

4.3.3.1. Behavioural Data

A baseline pre-test proprioceptive judgment was obtained prior to stimulation and a post-test judgment after stimulation. The pre-test judgment errors were subtracted from the post-test judgment errors prior to analysis. We use the term "proprioceptive drift" to refer to this quantity. A positive proprioceptive drift represents a mislocalisation towards the rubber hand. Figure 4-7 therefore shows the change in the perceived position of the hand between the start and end of the stimulation period, across the four conditions for n=10.

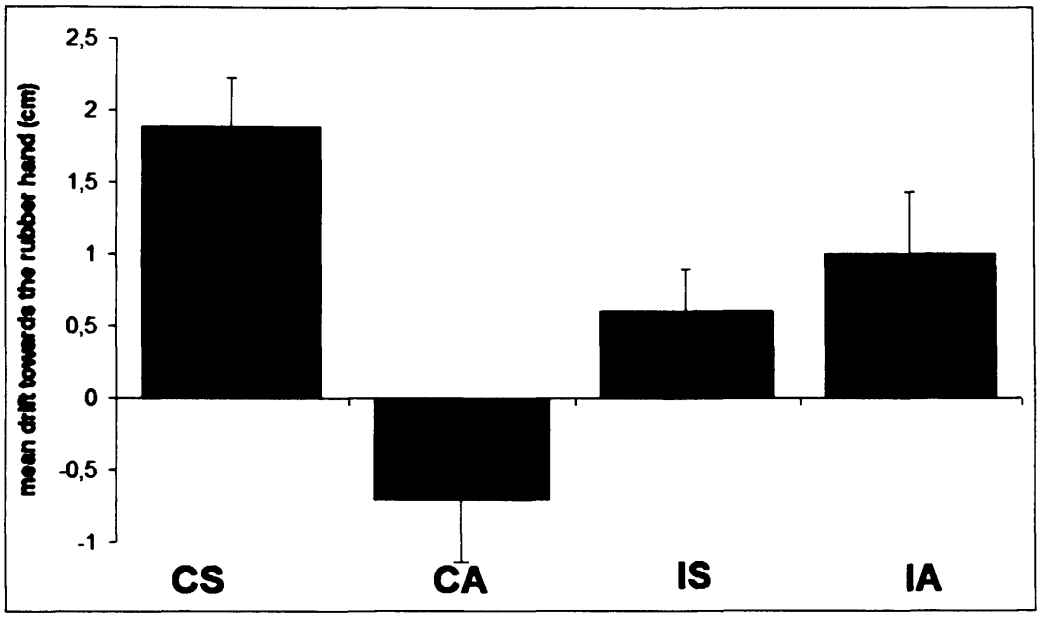

Figure 4-7. Mean proprioceptive drifts across conditions. Error bars indicate standard errors. Point "zero" represents the felt position of the participant's hand prior to stimulation. (CS: Congruent Hand/Synchronous Stimulation, CA: Congruent Hand/Asynchronous Stimulation, IS: Incongruent Hand/Synchronous Stimulation, IA: Incongruent Hand/Asynchronous Stimulation)

The mean proprioceptive drifts were submitted to a 2x2 Repeated Measures ANOVA with two within-subjects factors. The first factor was the Rubber Hand Identity (congruent vs. incongruent), and the second factor was the Mode of Stimulation (synchronous vs. asynchronous). The main effect of the Rubber Hand Identity was not significant ($F(1,9)=.005$ $p>0.05$). The main effect of the Mode of Stimulation was significant ($F(1,9)=7.397$, $p<0.05$). Importantly, the interaction of the two factors was highly significant ($F(1,9)=50.922$ $p<0.05$). These findings confirm the results of Experiment 4.2, namely that the RHI occurs only in the Congruent Synchronous Condition.

4.3.3.2. Introspective Evidence

After the scanning session, participants completed a questionnaire based on a previous questionnaire devised by Botvinick and Cohen (1998). The questions referred only to the synchronous conditions for each rubber hand identity condition (i.e. congruent rubber hand identity vs. incongruent rubber hand identity). Table 4-1 presents the mean subjective ratings for each question.

Table 4-1 Mean subjective ratings.

Mean Subjective Ratings for n=9[1] (The nine statements that the subjects had to deny (negative values), affirm (positive values) or report that they neither could confirm nor deny (0) are given.)			
	Congruent Rubber Hand Identity		**Incongruent Rubber Hand Identity**
When I was looking at the **rubber hand**, it seemed as if I were feeling the touch of the paintbrush in the location where I saw the fake hand being touched	0.55	***p*<0.05**	-0.66
When I was looking at the **rubber hand**, it seemed as though the touch I felt was caused by the paintbrush touching the rubber hand	0.11	*p*>0.05	-0.44
When I was looking at the **rubber hand**, I felt as if the rubber hand were my hand	0.44	***p*<0.05**	-1.22
When I was looking at the **rubber hand**, it felt as if my (real) hand were drifting towards the rubber hand	-0.44	***p*<0.05**	-1.44
When I was looking at the **rubber hand**, it seemed as if I might have more than one hand or arm	-1.77	*p*>0.05	-1.88
When I was looking at the **rubber hand**, it seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand	-1.33	*p*>0.05	-1.44
When I was looking at the **rubber hand,** it felt as if my (real) hand were turning 'rubbery'	-1.44	*p*>0.05	-1.66
When I was looking at the **rubber hand,** it appeared (visually) as if the rubber hand were drifting towards my hand	-2.33	*p*>0.05	-2.44
When I was looking at the **rubber hand,** the rubber hand began to resemble my own (real) hand, in terms of shape , skin tone, freckles or some other visual feature	-1.44	*p*>0.05	-1.88
[1]One subject did not complete the questionnaire.			

The introspective data suggest that subjects experienced the illusion only when they were looking at a congruent rubber hand identity. In particular, they affirmed that (i) they felt as if they are feeling the touch coming from the location where the congruent rubber hand was being touched, (ii) they felt as if the rubber hand was their own hand, and (iii) it was as if their own hand was drifting towards the rubber hand. These introspective data replicate previous studies (Botvinick & Cohen, 1998; Ehrsson et al., 2004), and they are compatible with the behavioural data collected in this study.

4.2.3.3. PET Data

Table 4-2 shows show the local maxima of the brain areas of increased neural activity at $p<0.001$ (uncorrected), as assessed by PET rCBF measurements, associated with the main effects of the 2x2 factorial design.

Table 4-2 Local maxima of the areas of differentially increased neural activity associated with the main effect of the experimental design. (L=Left, R=Right, SVC=Small Volume Correction)

Brain Regions	**MNI Coordinates**			**Peak T-value***
	x	*y*	*z*	
Main Effect of Synchronous Stimulation (CS+IS)-(CA+IA)				
L middle frontal sulcus	-20	26	34	4.53
R inferior lingual gyrus	6	-64	-6	3.41
Main Effect of Asynchronous Stimulation (CA+IA)-(CS+IS)				
Thalamus	-2	-2	0	6.09**
R rolandic operculum	52	-20	22	5.59**
L superior postcentral sulcus	-24	-50	72	4.07
L postecental gryus	-24	-42	74	3.95
L superior frontal sulcus	-30	0	68	3.94
R superior temporal sulcus	42	0	-20	3.51
Main Effect of Congruent Rubber Hand Identity (CS+CA)-(IS+IA)				
R precentral gyrus	66	4	26	3.98
R putamen	30	-6	6	3.82
L superior occipital gyrus	-26	-94	24	3.55
Main Effect of Incongruent Rubber Hand Identity (IS+IA)-(CS+CA)				
L amygdala	-28	6	-28	3.72
L parahippocampal gyrus	-32	-40	-8	3.62
R amygdala	32	-2	-28	3.56
Interaction Effect (CS-CA)-(IS-IA)				
R Cingulate	8	20	36	3.58
Conflict Interaction Effect (CA-CS)-(IA-IS)				
L Postcentral gyrus	-52	-26	62	3.85
L Precentral sulcus	-28	-12	64	3.74
R Opercular Inferior Frontal Gyrus	44	0	14	3.59***

*p<0.001 uncorrected, ** p<0.05 FWE corrected, ***p<0.05 after SVC following Fink et al (1999)

Main Effect of Synchronous stimulation

No significant activations were found ($p<0.05$) for the main effect of synchronous stimulation, corresponding to the contrast (CS+IS)-(CA+IA).

Main Effect of Asynchronous stimulation

The main effect of asynchronous stimulation corresponding to the contrast (CA+IA)-(CS+IA) showed significant activations ($p<0.005$ corrected for multiple comparisons over the whole brain) in the left thalamus (x=-2, y=-2, z=0, Z-score=5.58) and the right rolandic opreculum (x=52, y=-20, z=22, Z-score=5.19).

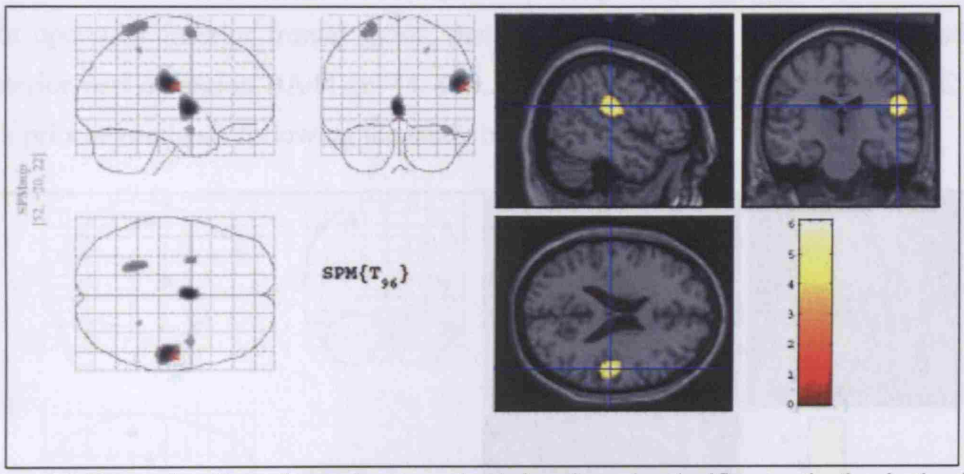

Figure 4-8 The main effect of asynchronous stimulation showed a significant activation in the right secondary somatosensory cortex (x=52, y=-20, z=22)

Main Effect of Congruent Identity

The main effect of looking at a congruent rubber hand being stimulated showed activity in the right precentral gyrus (x=66, y=4, z=26 $p<0.001$ uncorrected)

Main Effect of Incongruent Identity

The main effect of looking at an incongruent identity showed a bilateral activity in amygdala (x=-28, y=6, z=-28 and x=32, y=-2, z=-28, $p<0.001$ uncorrected).

Illusion Interaction Effect

The illusion interaction term of the factorial design was assessed using the contrast (CS-CA)-(IS-IA). No significant activations ($p<0.05$, corrected) were found for this interaction.

Conflict Interaction

To investigate the brain activity related to the conflict interaction term of the factorial design, we used the contrast (CA-CS)-(IA-IS). This contrast reveals brain activity during the conflict between what the subject feels and what he sees that cannot be accounted for by the summation of the effects of feeling asynchronous stimulation and seeing a rubber hand of an incongruent identity. Such activity was detected in the right opercular inferior frontal gyrus, that corresponds to the ventral lateral and most posterior part of region BA44 (x=44, y=0, z=14, Z-score=3.34 $p<0.05$ after SVC based on a priori hypothesis following the study by Fink et al., 1999).

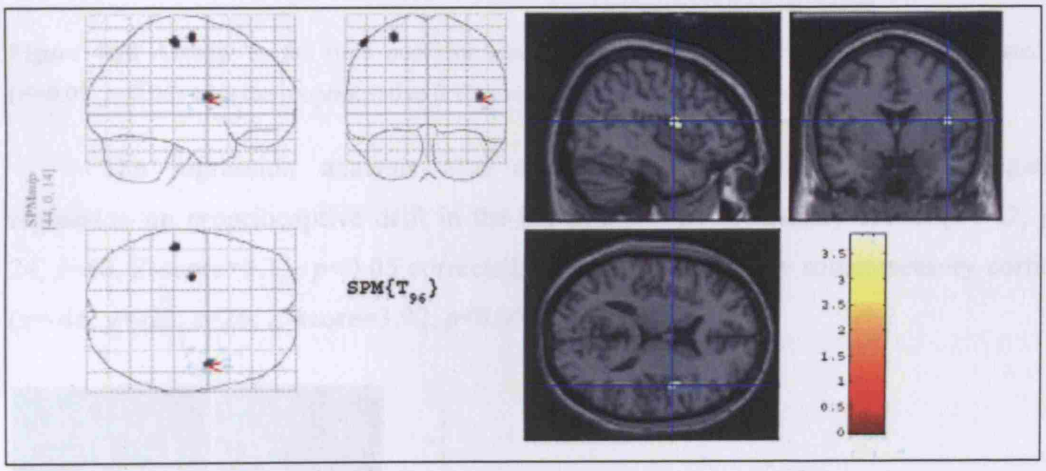

Figure 4-9 Activity in the posterior part of BA44 (x=44, y=0, z=14).

4.2.3.4. Correlation of Neuroimaging and Psychophysical Data

The effects of global changes in blood flow between conditions were modelled as a confound using a subject-specific ANCOVA. SPM2 was used to identify brain areas where activity was predicted by the proprioceptive drift. To this end, the proprioceptive drift was used as a covariate and a linear regression with this covariate was calculated for every voxel in the whole brain. This analysis focuses on the effects of the illusion, rather than on the conditions which caused it.

The regression analysis demonstrated a significant positive regression on proprioceptive drift in the right posterior insula (x=44, y=-10, z=14, Z-score=3.63, p<0.05 SVC) and in the right frontal operculum (x=58, y=12, z=-4, Z-score=3.47 p<0.05 SVC).

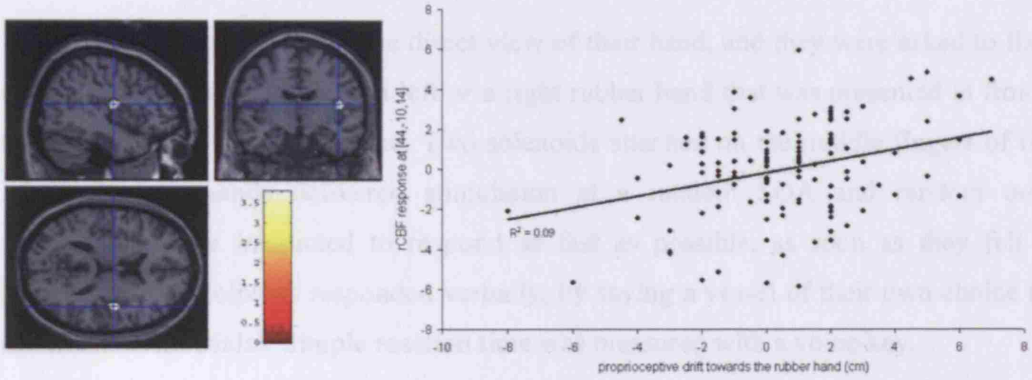

Figure 4-10 Activity in the right posterior insula (x=44, y=-10, z=14) was positively correlated (r^2=0.09, p<0.05) with the proprioceptive drift towards the rubber hand.

The regression analysis also demonstrated a highly significant negative regression on proprioceptive drift in the left primary somatosensory cortex (x=-42, y=-24, z=40, Z-score=5.11, p<0.05 corrected,) and in the secondary somatosensory cortices (x=-46, y=-22, z=26, Z-score=3.92, p<0.05 corrected).

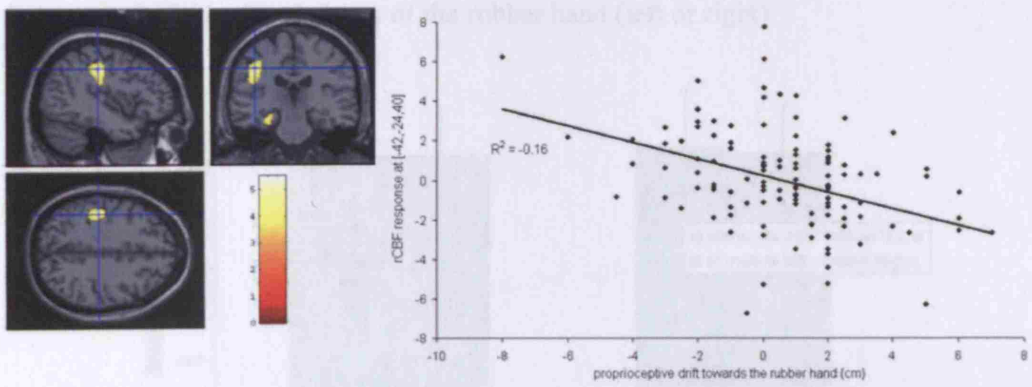

Figure 4-11 Activity in the left somatosensory cortex (x=-42, y=-24, z=40) was negatively correlated (r^2=0.16 p<0.05) with the proprioceptive drift towards the rubber hand.

4.2.3.5. Control Experiment

Prior to the main experiment, a control experiment was performed in order to ensure that simply looking at a left or a right rubber hand would not bias tactile attention on the subject's own left or right hand. The design was 2x2 factorial. Participants were stimulated either on their left or right middle finger, while they were looking at a left or a right rubber hand.

Participants did not have direct view of their hand, and they were asked to fixate on the middle finger of either a left or a right rubber hand that was presented in front of them, aligned with their midline. Two solenoids attached on the middle fingers of their left and right hands delivered stimulation at a random SOA and random order. Participants were instructed to respond as fast as possible, as soon as they felt the stimulation. Participants responded verbally, by saying a vowel of their own choice (the same across all trials). Simple reaction time was measured with a voice-key.

The experimental design resulted in four conditions, and 20 trials were run for each condition. The order of the presentation of the left or right rubber rand was counterbalanced across subjects. Sixteen new participants (9 females, mean age 23, all right handed) took part in this experiment.

The median RTs (see Figure 4-12) were submitted to a 2x2 Repeated Measures ANOVA, with two within-subjects factors: (i) the finger stimulated (left or right middle finger), and (ii) the handedness of the rubber hand (left or right).

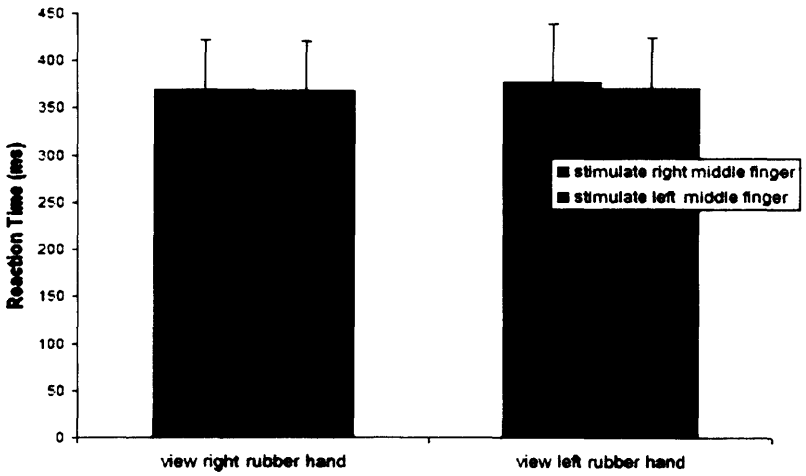

Figure 4-12. Median Reaction Time in ms across conditions for the Control Experiment. Error bars represent standard deviations.

None of the main effects were significant (main effect of finger stimulated: $F(1,15)=0.793$, $p>0.3$, and main effect of handedness of the rubber hand: $F(1,15)= 0.624$, $p>0.4$). The interaction of the two factors did not reach significance either $F(1,15)=0.812$, $p>0.3$). Thus, simply looking at a left or a right rubber hand do not bias tactile attention to the subject's own stimulated hand.

4.3.4. Discussion

The main purpose of this study was to investigate the neural and functional signatures of body-ownership and dis-ownership by using the paradigm of the Rubber Hand Illusion (RHI). In particular, the focus was on the correlation between neural activity and the phenomenal experience associated with the RHI. In this study three main findings were reported. Activity in the posterior part of area BA 44, close to BA6, is involved in detecting a conflict between visual, tactile and proprioceptive signals. The phenomenal incorporation of a rubber hand is reflected in activity in the right posterior insula and the right frontal operculum. Conversely, a discrepant body experience, namely the dis-ownership of the rubber hand is related to activity in the contralateral primary and secondary somatosensory cortices.

There has been only one previous neuroimaging study investigating the neural correlates of body-ownership using the RHI paradigm (Ehrsson et al., 2004). In that study, the experience of the RHI showed increased activity in the bilateral ventral premotor cortex and bilateral frontal operculum. The present study replicated the activation in the frontal operculum, in the right hemisphere, but it failed to show activity in premotor cortex. This can be accounted by differences in the methodologies and experimental designs of the two studies. Ehrsson and colleagues used short blocks of visuo-tactile stimulation (42 seconds). That enabled the investigation of the temporal evolution and the dynamic process of recalibration of hand position that occurs shortly before (~11secs) and shortly after the illusion (~31secs). In fact, activity in the premotor cortex in their study was related to the onset of the experience of the illusion.

One can distinguish between the incorporation process (Ehrsson et al., 2004), and the state of being incorporated/owned as in the present study. In the present study, acquisition of the neuroimaging data begun after the first 45 seconds of visuo-tactile stimulation, because the focus here was on the correlation between neural activity and the sustained experience of the illusion as measured by the proprioceptive drifts. Previous data suggest that the proprioceptive drift towards the rubber hand increases steadily for approximately 3 minutes (see Experiment 5.2 in Chapter 5, and Tsakiris & Haggard, 2005b). That would suggest that the phenomenal experience of the illusion is stronger after longer periods of synchronous stimulation. It is unknown whether

sustained activity in the premotor cortex would last for prolonged stimulation periods, or whether premotor activity reflects the dynamic aspects or the end-result of the visuo-tactile correlation. In the present study, the low temporal resolution of PET did not allow the investigation of the dynamic changes in brain activity related to the period before and after the illusion as in the study by Ehrsson et al (2004). Instead, the main focus was on the neural activity related to the experience of ownership.

The experience of ownership of the rubber hand

The experience of ownership of the rubber hand as measured with proprioception was positively correlated with right hemispheric activity in the posterior insula and the frontal operculum. These two areas are reciprocally connected through efferent and afferent projections (for a review see Augustine, 1996). Bilateral frontal operculum activity was found by Ehrsson et al. (2004) when subjects experienced the RHI. Insular activity has been consistently implicated in self-attribution. In a neuroimaging study on agency, Farrer and colleagues (2003a) showed that activation in a very similar location as in our study (x=44, y=-10, z=14 in the present study, and x=40, y=-10, z=16 in Farrer at el., 2003a) decreased when subjects experienced a discordance between what they did and what they saw, suggesting that activity in the posterior insula correlates with the degree of congruence between different signals and self-attribution.

The functional characterization of the insular lobe has shown that the insula is a multi-faceted sensory-motor area, involved in both visceral and peripheral somatosensation (for a review see Augustine, 1996). The insula is divided by the central insular sulcus into an anterior and posterior part. The anterior part has more extensive connections with limbic, paralimbic, olfactory, gustatory, and autonomic structures. The posterior part is more closely connected to somatosensory, auditory, and motor areas (Mesulam and Mufson, 1985). The major connections of the posterior insula include those with primary and secondary somatosensory cortex (SI, SII), superior and inferior parietal lobule, orbitofrontal, prefrontal, and premotor cortex, auditory cortex, superior and inferior temporal cortex, as well as with the basal ganglia and thalamus (Mesulam and Mufson, 1985; Augustine,1996).

The suggestion that the posterior insula is involved in the network integrating signals related to self-awareness and our beliefs about function and ownership of contralateral body parts is further supported by a series of recent studies. Activity in the

insula has also been found in numerous studies involving self-processing. Fink et al. (1996) reported an activation of the anterior–midposterior insula when subjects identified their own memories. Kircher et al. (2000, 2001) observed anterior insula activation when subjects had to recognize their own face or recognize descriptions of themselves in words. Farrer and Frith (2002) have already proposed that the sense of agency is associated with a shift of attention towards representations that integrate multiple body- and action-related signals, and that this integrating process might involve the insula. The present study extends these findings by showing a correlation between activity in the insula and self-attribution of a body-part. Importantly, though, the present study, contrary to previous studies where posterior insula was activated during self-attribution of actions, shows that posterior insula is active even in the absence of efferent information. This fact may suggest that in previous studies, the activity in the insula that was associated to action-attribution may in fact reflect body-ownership and not agency.

Interestingly, in a recent lesion mapping study, Karnath, Baier & Naagele (2005) showed that the right posterior insula is commonly damaged in patients with anosognosia for hemiplegia/hemiparesis but is significantly less involved in hemiplegic/hemiparetic patients without anosognosia (see also Berti et al., 2005; Cereda et al., 2002). The present finding supports the hypothesis that the insular cortex is integral to self-awareness and to one's beliefs about the functioning of body parts.

The experience of dis-ownership of the rubber hand

The negative correlation between the proprioceptive drift and the rCBF revealed a significant activation in the left parietal cortex, in particular in the primary and secondary somatosensory cortices. The behavioural correlate of the attribution of the rubber hand to one's own body is a change in the perceived location of the subject's hand towards the rubber hand. To that extent, the larger the proprioceptive drift is, the more powerful the illusion is experienced. Therefore, small proprioceptive drifts indicate a failure to attribute the rubber hand to one's own body, presumably because of a discrepancy between the proprioceptive experience of the subject's own hand, and the visual perception of the rubber hand. The negative correlation between activity in the somatosensory cortex and proprioceptive drift reflects the phenomenal experience of dis-ownership of the rubber hand, and it suggests that the left parietal cortex is particularly

involved in signalling or maintaining the felt location of the hand against conflicting visual input.

A recent study by Keysers et al., (2004) found activation in SII when subjects watched someone else being touched (see also Blakemore et al., 2005). This finding seems compatible with the "not me" quality of the dis-atrribution condition in the present study. Thus, activity in SI and SII might reflect the persistence of the conflict between the felt position of the subject's hand and the viewed location and identity of the rubber hand. In particular, the somatosensory cortex may be involved in the maintenance of an internal reference body-representation and the preservation of the body/world boundary, as opposed to the process of a new assimilation or reconstruction of the body. In a series of recent studies, Schaeffer and colleagues (2005a,b,c) demonstrated an active involvement of S1 in the referral of tactile sensations to an alien limb. In one study (Schaefer et al., 2005c), subjects were stimulated on D1 while they watched a video image of hand being stimulated on D5. Neuromagnetic source imaging of the topography of the functional organization of SI related to tactile stimulation of D1 and D5 showed that the source extent of the cortical representation of D5 increased during the observation of the video image of the hand that was stimulated synchronously with the subject's hand. The authors also reported that the subjects experienced feeling as being touched on their fifth digit (D5), rather than on their first digit. In that study, primary somatosensory cortex was found to be critically involved in the processing of visuo-tactile integration and visuo-tactile enhancement (see also Kennet et al., 2001, Press et al., 2004). However, it seems unlikely that the somatosensory cortex is actually involved in the phenomenal experience of self-attribution or body-ownership per se. The neuropsychological literature suggests that self-attribution or dis-attribution of body-parts does not follow after damage to the primary somatosensory cortex (see section 1.4.1). According to Schaefer and colleagues the effects observed in S1 may be caused by top-down projections from multimodal parietal areas.

The posterior parietal cortex and the secondary somatosensory cortex have also been shown to be active when subjects observe impossible hand movements. Costantini and colleagues (2005) investigated the brain activity during observation of impossible or possible hand movements. An increase in rCBF linked to observation of impossible versus possible hand movements was found in sensorymotor parietal regions, in

particular in left SII (x=-64, y=-20, z=28), and right posterior parietal cortex. This result is particular relevant to the manipulation of the rubber hand identity in the present design. When subjects were looking at a left rubber hand being stimulated, while their own right hand was stimulated, the very possibility of the left rubber hand being incorporated at the location and possibly at the expense of the subject's right hand would violate a stored reference of the subject's own body. What can we speculate about the functional role of the somatosensory cortex? It may be suggested that the somatosensory cortex, because it maintains a stored reference of the body, is particularly sensitive to handedness (i.e. left vs. right hand manipulation), to the kinaesthetic proprioceptive space (i.e. proprioceptive drift), and to both visual and tactile inputs (see also Schaeffer et al., 2005a,b,c).

As shown in the behavioural data (Figure 4-7), the smallest proprioceptive drifts were observed in the Congruent Asynchronous condition. Interestingly, the main effect of asynchronous stimulation, but also the simple main effect of the contrast CA-CS, showed an activation in the left superior parietal lobule (x=-24, y=-50, z=72, Z-score=3.9 $p<0.001$ uncorrected). It has been reported that one of the functional roles of the left superior parietal lobule is body-part localization. In a recent fMRI study, Felician and colleagues (2004) showed a selective activation of the left superior parietal lobule at similar coordinates to the present study (x=-18, y=-50, z=72, see Felician et al., 2004) when subjects were asked to localize their body parts. However, the fact that in the present study, we did not observe significant activations in the inferior and superior parietal lobes can be accounted by the intrinsic properties of the RHI. The inferior parietal lobe is involved in action-recognition and action-attribution, while the superior parietal lobe has been associated with the coding of the egocentric space. On the contrary, the RHI is a passive situation and it does occur in the body space.

The factorial design of present study was also used to investigate the neural responses related to a conflict between body-related sensory signals. In the present study, dis-ownership is based on the interaction of the factorial design, according to which visual and tactile percepts are congruent but they are in conflict with the kinaesthetic body reference frame (see interaction (CA-CS)-(IA-IS) in section 4.2.3.3). This interaction showed that a lateral area found in the opercular inferior frontal gyrus, corresponding to the posterior part of BA44, was active when participants experience a

conflict between proprioception, touch and vision. The functional role of this area would be to detect and resolve various conflicting signals between internal and external representations of body-related events. This is in accordance with previous studies. Fink et al. (1999) used a mirror to manipulate visual feedback, while subjects performed the Luria bi-manual coordination task. Participants were instructed to open and close both hands repetitively, either in-phase or out-of-phase, while observing their hand movements. A mirror was used to manipulate the visual feedback. In some conditions, the participant's intention and proprioceptive feedback indicated out-of-phase hand movements, while the mirror showed in-phase hand movements. The mismatch between intention, proprioception and vision activated the right DLPFC. In particular, a dorsal area (BA 9/46) in right lateral prefrontal cortex was activated when actions had to be maintained in the face of a conflict between intention and sensory feedback. In a second experiment, where the active movements were replaced by passive movements, a right ventral lateral prefrontal region (BA 44/45), anterior from the peak of activation reported in the present study, was primarily activated by discrepancies between signals from the different sensory systems. The difference in the location of the peak of activation reported in the present study might be accounted by the fact that in the present design the conflict was between purely afferent events (i.e. vision, touch and proprioception), whereas in the study by Fink and colleagues (1999), the conflict was between visual feedback and active movement in Experiment 1, and between visual feedback and passive movement in Experiment 2.

A recent study by Berti and colleagues (2005) showed that anosognosia for hemiplegia is associated to lesions in the insula (see also Karnath, Baier & Naagele, 2005), but also to lesions in BA44 and BA6. One interpretation offered by the authors is that the denial of motor deficits arises, in part, by a failure to monitor the signals related to the movement. One consequence of that failure would be to "ignore" the conflict between signals related to the intended and the actual states of the limbs, resulting in anosognosia. The activation reported in Experiment 4.3 in an area located at the posterior part of BA44, close to BA6 is compatible with the suggestion that this area is critical for the monitoring of various bodily-related signals.

4.4. Body-ownership is an interaction

In a series of experiments, participants perceived their hand to be closer to the rubber hand after synchronous visual and tactile stimulation, as an effect of integration between the visually-perceived rubber hand and the tactile experience on the subject's own hand. However, not all multisensory stimuli were experienced as part of the body, suggesting that the correlation of visual and tactile percepts is a necessary, but not sufficient, condition for the sense of ownership. This was confirmed in Experiment 4-2, in which subjects were always stimulated on their left hand, while they were looking at a left or a right rubber hand. When subjects were looking at a congruent rubber hand identity (i.e. a left rubber hand), they perceived their hand to be significantly closer to the rubber hand after synchronous stimulation than after asynchronous stimulation. Conversely, when subjects were looking at an incongruent rubber hand identity, differences in the proprioceptive judgments between synchronous and asynchronous conditions were not significant. That is, synchronous stimulation between the participant's left hand and a right rubber hand did not induce the illusion. The viewed object therefore needs to fit with a general pre-existing representation of the body scheme (see Experiment 4-1). Thus, a second factor that seems to modulate body-ownership is top-down influences originating from prior visual, proprioceptive and functional representations of the body.

Experiment 4.3 investigated the neural signatures of body-ownership using the Rubber Hand Illusion. The experimental design was based on Experiment 4-2. The bottom-up processes that drive the RHI were operationalized in the pattern of visuo-tactile stimulation (i.e. synchronous vs. asynchronous stimulation), whereas the top-down influences that modulate the RHI were operationalized in the manipulation of the rubber hand identity. Body-ownership was defined as the interaction between these two factors, and it was validated using a behavioural proxy (i.e. the proprioceptive drift). This approach allowed the distinction between the causes and the effects of the RHI. With regards to the neural processes, Experiment 4.3 showed that the posterior part of BA44 is involved in detecting discrepancies between visual, tactile and proprioceptive bodily-related signals. The right posterior cortex and in particular the right SII was involved in the processing of selective discrepant features of body-specific stimulation such as the asynchronicity between visual and tactile percepts. With regards to the neural signatures

of body-ownership, the results showed a strong correlation between activity in the right posterior insula and frontal operculum and the strength of the illusion as measured by proprioceptive drift. When the rubber hand was not attributed to the self, activity was observed in left parietal somatosensory cortex. Overall, the neural correlates of the RHI suggest that the sense of ownership is related to activity in the right posterior insula and the right frontal operculum. Conversely, the sense of dis-ownership, that an object is not linked to the body, was related to increased activity in the left parietal cortex, in particular the primary and secondary somatosensory cortices. Finally, the fact that no significant brain activations were associated with the illusion interaction (CS-CA)-(IS-IA) suggests that ownership may be a default mode of the brain's sense of self.

5. Body-awareness: the Sensory and the Acting Self [4]

5.1. The Sensory Self

In the previous chapter, self-attribution and body-ownership of a rubber hand was defined as the result of an interaction between bottom-up processes of multisensory stimulation and top-down cognitive representations of the body. One example that illustrates this interaction was provided in Experiment 4.2: subjects perceived their hand to be closer to the rubber hand *only* when the rubber hand was of congruent identity with respect to the subject's stimulated hand.

Another interesting finding of Experiment 4.2 was that significant proprioceptive drifts towards the rubber hand were induced only for the stimulated finger of the participant's hand. Indeed, when participants were asked to judge the felt position of their stimulated middle finger, they perceived it to be significantly closer to the rubber hand than it really was. However, when they were asked to judge the felt location of their *un*stimulated thumb finger, they did not perceive it to be significantly closer to the rubber hand than it really was (see Figure 4-4). Thus, the perceived position of the unstimulated finger did not drift, even after the synchronous condition. This finding suggests that the RHI may induce a distortion of the hand scheme, because, after synchronous stimulation, only the stimulated finger "leaves" the subject's hand, in the sense that only that finger is perceived to be in a different location in space, that is, closer to the rubber hand.

On one view, the pattern of localized proprioceptive drifts provides support for a Bayesian view of the self because stronger statistical correlations are expected only for the stimulated finger (see section 4.2.4). According to the Bayesian account (Armel & Ramachandran, 2003), the bodily self is merely the product of a regularly reinforced pattern of somatic sensations. The strong version of the Bayesian model postulates that the body scheme is constructed on the basis of visuo-tactile integration. Therefore, the pattern of localized proprioceptive drifts, which reflects a distortion of the hand scheme, can be explained by the nature of localized visuo-tactile stimulation. On another account, body-representations modulate the integration of visuo-tactile percepts, suggesting that

[4] Experiments 5.1. and 5.2 were published in Tsakiris M & Haggard P (2005a). The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance* **31**(1):80-91.Experiment 5.3 was published in Tsakiris M, Prabhu G & Haggard P (2005). Having a body versus moving your body: how agency structures body-ownership. *Consciousness & Cognition*, in press.

body-ownership in the RHI arises as an interaction between bottom-up processes of multisensory integration and top-down influences originating from cognitive representations of the body (see Chapter 4). Experiment 4.2 provided support for both the bottom-up and the top-down accounts. For example, in Experiment 4.2, the stimulated finger was perceived to be closer to the rubber hand, when the rubber hand was of congruent identity with respect to the participant's hand, but it was not perceived to be closer to the rubber hand, when the rubber hand was of an incongruent identity. At the same time, when subjects were looking at a congruent rubber hand, and they were asked to judge the perceived position of their unstimulated thumb finger, they did not perceive their thumb finger to be closer to the rubber hand than it really was.

However, one confounding factor in Experiment 4.2 was the fact that across all conditions only one finger was stimulated. Thus, it remains unclear whether this pattern of localized proprioceptive drifts reflects an artefact of attention directed to the stimulated digit or whether it reflects a fragmented body-awareness induced with the passive visuo-tactile stimulation. Experiments 5.1 and 5.2 were designed to further investigate this hypothesis. In particular these two experiments focused on the perceptual process of multisensory integration that builds-up to the inducement of the illusion and the effects of this integration on proprioceptive awareness (i.e. an alteration on the perceived position of the subject's hand).

5.1.2. Experiment 5.1

5.1.2.1. Experimental Design & Methods

Experimental Design

Experiment 5.1 was designed to further investigate the localized proprioceptive drifts of RHI seen in Experiment 4.2. The experimental design was 2x2x2 factorial. The 3 factors were:

(i) the mode of stroking (synchronous vs. asynchronous),

(ii) the finger stimulated (index vs. little), and

(iii) the finger judged (index vs. little).

Figure 5-1 shows the experimental design and the experimental set-up.

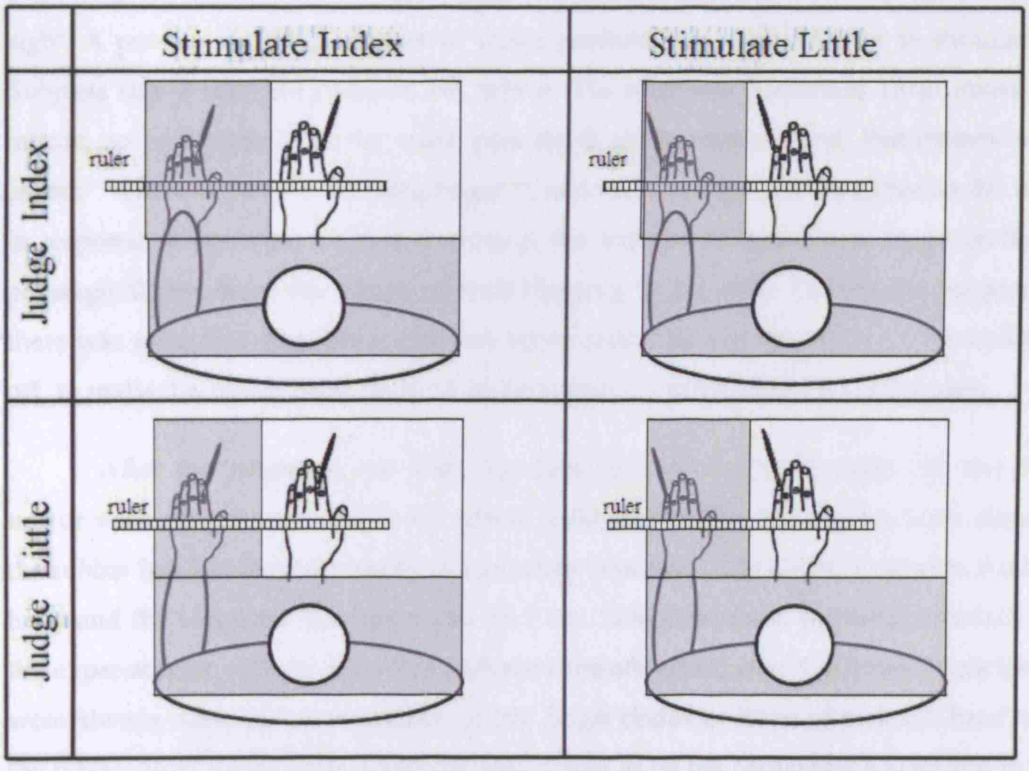

Figure 5-1 Experiment Design and set-up.

Only one finger was stroked per condition (the index or the little), always the same as the one on the rubber hand. Participants were asked to judge the position of either the stimulated or the unstimulated finger. Only the fingers of the left hand were stimulated, and participants always watched a left rubber hand, being stroked at the exact same location as their own left hand.

There were 4 experimental (i.e. synchronous) and 4 control (i.e. asynchronous) conditions. The conditions were blocked, and randomly ordered between subjects. Stimulation was delivered horizontally on the index finger or the little finger.

Methods

Participants sat in front of a table. At the beginning of each block, their left hand was placed by the experimenter at a fixed point inside a frame, whose top-side was covered by one-way and two-way mirrors. The two-way mirror was used to make the rubber hand appear (during stimulation) and disappear (during judgment). At the beginning of each block, both the participant's left hand and the rubber hand were out of sight. A pre-test baseline estimate of finger position was obtained prior to stimulation. Subjects saw a ruler reflected on the mirror. The ruler was positioned 18cm above the mirror, so as to appear at the same gaze depth as the rubber hand. Participants were asked: "Where is your index/little finger?", and verbally reported a number on the ruler in response. They were instructed to judge the position of their finger by projecting a parasagittal line from the centre of their fingertip to the ruler. During the judgments, there was no tactile stimulation, and the lights under the two-way mirror were switched off, to make the rubber hand invisible to the subjects, leaving only the ruler visible.

After the judgment, the ruler was removed, and the lights under the two-way mirror were turned on, to make the rubber hand appear. The participants were viewing the rubber hand in the same depth plane as their own hand. The distance between the real hand and the viewed rubber hand was 17.5 cm. Stimulation was delivered manually by the experimenter with the use of two identical paintbrushes, over 4 minutes. Participants were always stimulated horizontally on one finger (index or little) of their left hand, and the rubber hand was stimulated on the same finger as on the participant's hand and in the same way. Both the participant's hand and the rubber hand wore identical elastic gloves, to eliminate visual, tactile and auditory differences. In the synchronous conditions, both

the participant's hand and the rubber hand were stroked simultaneously and at the same location. Stimulation was delivered manually along the index or little finger from the knuckle to the fingertip. Each stroke lasted approximately 500ms-1000ms. The experimenter immediately repositioned the brush at the knuckle and began the next stroke some 500-1000 ms after the end of the previous stroke. In the asynchronous conditions, visual stimulation preceded tactile stimulation and the asynchrony was randomly varied between 500-1000ms.

After the stimulation period, the lights were automatically turned off. The ruler was always presented with a random offset to ensure that participants judged finger position anew on each trial, and that they could not simply repeat previous responses. Participants were asked "Where is your index/little finger?". After their answer the ruler was removed, and they were asked to move their left hand, and have a rest for a few moments. Following the rest period, their left hand was again passively placed at a pre-determined point, under the frame, and out of sight. The same process was followed for each condition, and there were two repetitions for each condition.

Participants

Ten right-handed volunteers (mean age 23, 7 female) with normal or corrected to normal vision, participated, after giving their informed consent. Subjects were naïve as to the purpose of the experiment, and had not prior knowledge or experience of the RHI. The study was approved by the local ethical committee.

5.1.2.2. Results

Figure 5-2 shows the mean proprioceptive drifts across conditions.

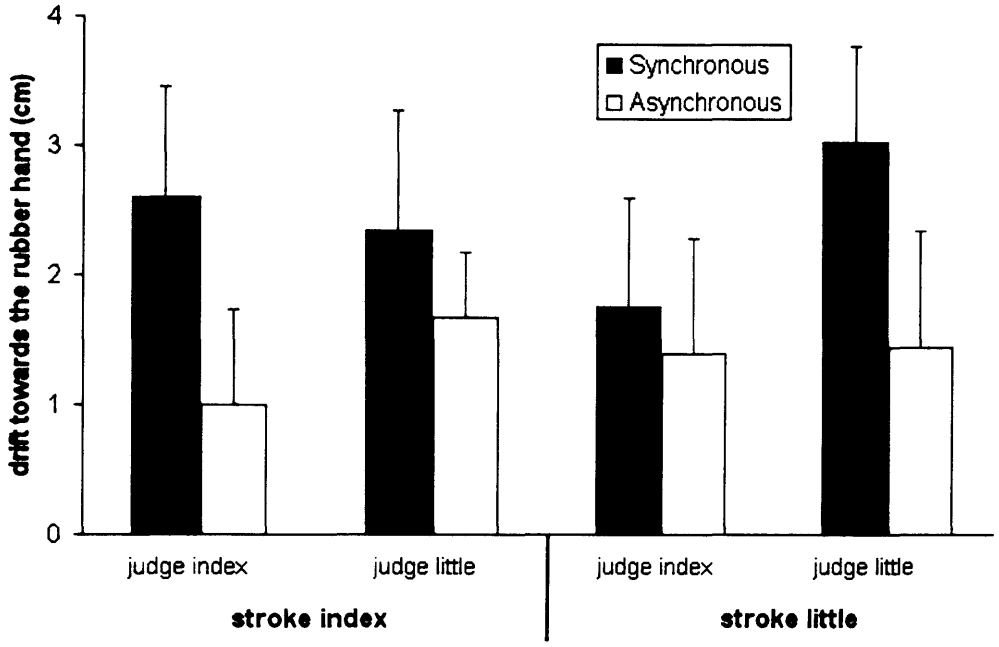

Figure 5-2 Mean proprioceptive drift across conditions. Error bars indicate standard errors. Point "zero" represented the felt position of the hand prior to the simulation.

The proprioceptive drifts across conditions were submitted in a 2x2x2 ANOVA with three within-subjects factors. The factors were (a) the finger stimulated (index vs. little), (b) the finger judged (index vs. little), and (c) the mode of stroking (synchronous vs. asynchronous). The main effect of "finger stroked" was not significant ($F(1,9)=.00$, $p>0.05$), nor was the main effect of "finger judged" ($F(1,9)=.44$, $p>0.05$). The main effect of the mode of stroking was significant ($F(1,9)=7.73$, $p<0.05$. Moreover, the interaction of the three factors was significant ($F(1,9)=6.07$, $p<0.05$).

Simple effects analysis (Howell, 1997) was used to compare the mean proprioceptive drifts between the synchronous and the asynchronous conditions. Differences were significant only when subjects judged the finger that had just been stroked (for the index finger, $t(9)=3.983$, $p<0.05$, and for the little finger, $t(9)=4.082$, $p<0.05$). When the finger judged was not the finger stroked, the drifts were not

significantly different for the two different modes of stroking ($t(9)=.637$, $p>0.05$ for the index, and $t(9)=.746$, $p>0.05$ for the little), suggesting that the RHI did not occur.

The main focus here is on the change due to visual-tactile integration. This component can be defined as the additional change in positional drift when visual and tactile stimuli are correlated (i.e. synchronous conditions), over and above the drift caused by the same stimuli when they are less clearly correlated (i.e. asynchronous conditions). Therefore, to obtain a more specific measure of the RHI, the proprioceptive drifts obtained in the asynchronous conditions were subtracted from the proprioceptive drifts obtained in the synchronous conditions. The term "perceptual shifts" refers to this quantity. The perceptual shifts were calculated by subtracting the proprioceptive drifts obtained for the asynchronous conditions from the synchronous ones. Figure 5-3 shows the mean perceptual shifts across conditions. Only the perceptual shifts for the conditions where the finger judged was the finger stroked were reliably greater than zero ($t(9)=4.082$, $p<0.003$, for the index, and $t(9)=3.98$, $p<0.003$, for the little).

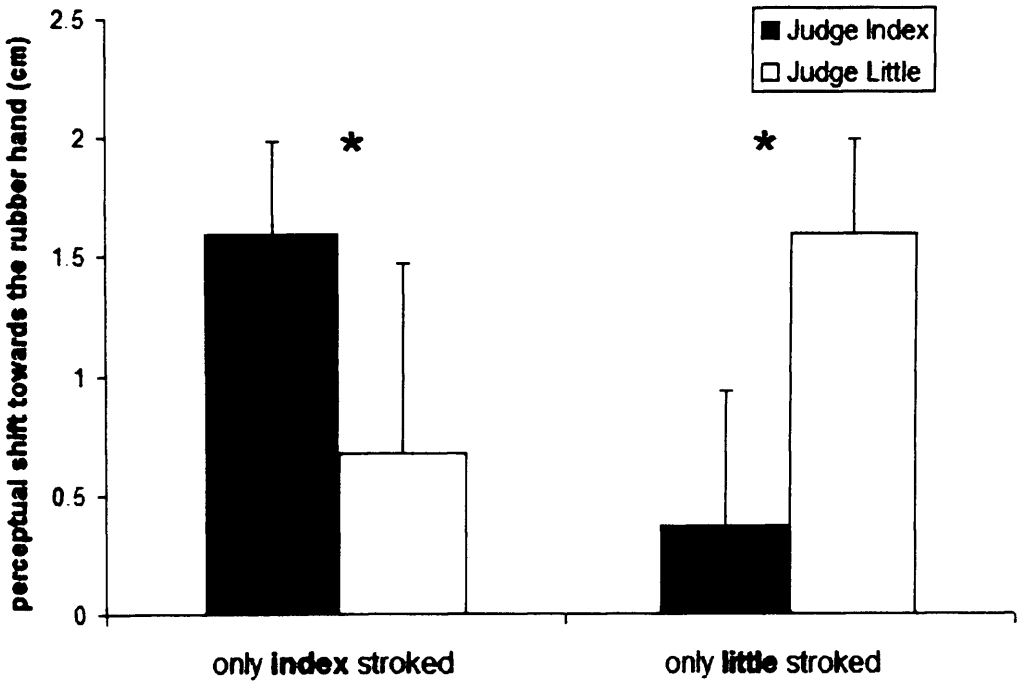

Figure 5-3. Mean perceptual shifts in Experiment 5-1. Error bars indicate standard errors. Asterisks indicate significant differences between judgments for the stimulated and the unstimulated finger.

The mean perceptual shifts were also submitted to a 2x2 Repeated Measures ANOVA with two within-subjects factors. The first factor was the Finger Stroked (index or little) and the second factor was the Finger Judged (index or little). The main effect of the Finger Stroked was not significant ($F(1,9)=0.047$, $p>0.05$), nor was the main effect of the Finger Judged ($F(1,9)=0.118$, $p>0.05$). However, the interaction of the two factors was significant ($F(1,9)=6.074$, $p<0.05$) because larger shifts occurred when judging the position of the stimulated finger compared to the unstimulated finger.

In order to further investigate whether differences in perceptual shifts across conditions could be accounted by an attentional bias towards the stroked finger, a repeated measures ANOVA was performed on the standard deviations of perceptual shifts across the 2 trials in each condition, with all the within-subjects factors included. If specificity of the RHI to the stimulated finger reflected attentional bias, rather than a true difference in the strength of the illusion, then the perceptual shifts might be more erratic for the unstimulated than for the stimulated finger. No significant differences were found.

These results replicate the finding of Experiment 4-2, namely a pattern of localized proprioceptive drifts, restricted to the stimulated finger only. Nevertheless, the pattern of results could arise because only one finger was stimulated in each condition. Thus, the localized pattern of result could arise as an artefact of tactile attention directed to the digit that was stimulated in each condition. To further investigate the local effect of proprioceptive drift obtained in this experiment, Experiment 5-2 was designed to provide a better control for possible attentional artefacts.

5.1.3. Experiment 5.2

The aim of experiment 5.2 was to improve the design of the previous experiment. To that extent, two fingers were always stimulated across all trials. In addition, to test whether the increase of the number of digits stimulated would produce a spreading pattern of drifts to other unstimulated digits, proprioceptive judgments were obtained for the two fingers that were stimulated, but also for a third digit that was never stimulated.

51.3.1 Experimental Design & Methods

In experiment 5-2, two fingers, the index and the little, were always stimulated across all trials, but the pattern of stimulation on each finger was manipulated independently to be either synchronous or asynchronous with respect to the corresponding finger of the rubber hand. Thus, the experimental factors were: (i) the mode of stroking, and (ii) the finger judged.

Mode of stroking

The index and the little fingers of the participants' left hand and of a left rubber hand were stroked in all conditions. The conditions differed only in the pattern of stimulation across the fingers (i.e. the index and the little). The rubber hand always received the same pattern of stimulation, to the index and little fingers simultaneously. However, the participants' index or little finger might or might not receive the same pattern of stimulation as the rubber hand. Thus, there were 4 different stimulation conditions of the subject's fingers:

(a) both index and little fingers on the participant's hand were stroked in synchrony with the index and little fingers of the rubber hand,

(b) the participant's index finger was stroked in synchrony with the rubber fingers, while the little finger was stroked asynchronously,

(c) the participant's little finger was stroked in synchrony with the rubber fingers, while the index finger was stroked asynchronously,

(d) both the participant's fingers were stroked asynchronously with respect to the rubber fingers.

Finger Judged

For each stimulation condition, participants had to judge, in different blocks, the position of (a) their index, (b) their little, or (c) their middle finger. The middle finger was never stimulated, but proprioceptive judgments obtained for the middle finger would be sensitive to any spreading of the proprioceptive drifts due to the increase of the number of digits stimulated, compared to Experiment 5.1.

Methods

Stimulation was delivered mechanically by two stepper motors (see Figure 5.4). Computer-controlled motors were used to ensure that the overall amount of stimulation was precisely matched across conditions. To simulate the unpredictable nature of manual stroking, the direction and speed of stroking were randomly varied within conditions. The subject's hand and rubber hand always received the same random direction and speed on each stroke. In the synchronous condition, the subject's hand and the rubber hand were stroked simultaneously. In the asynchronous conditions, the finger was stroked with a random delay of 500ms-1000ms after stroking of the rubber hand. The total amount and spatial pattern of stimulation was the same across all conditions. Synchronous and asynchronous conditions differed only in the degree of temporal correlation of visual and tactile stimulation.

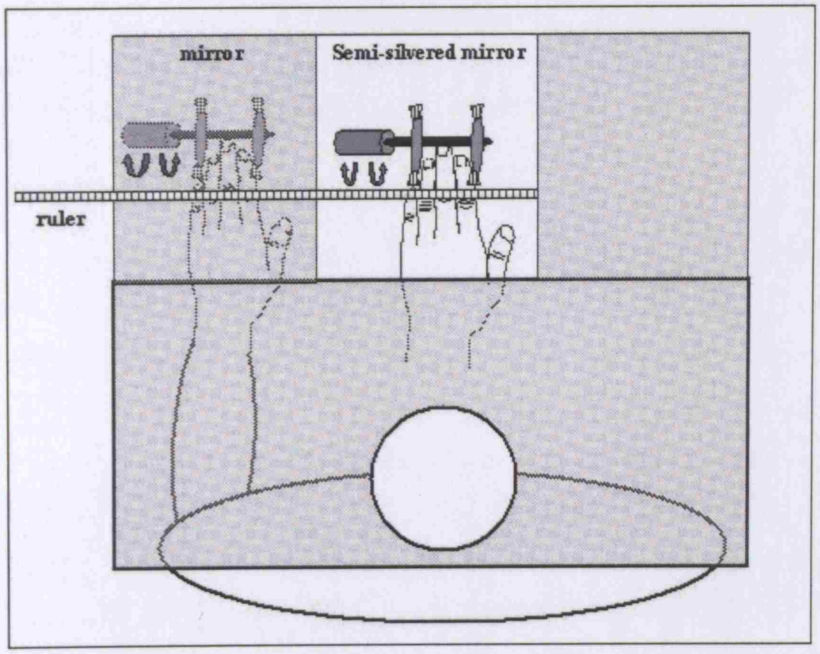

Figure 5-4. Experimental set-up used in Experiment 5-2.

Participants sat at a table. The rubber hand was presented in front of them, aligned with their midline. Participants could see the rubber hand through a two-way mirror. Before the start of each block, the rubber hand was invisible and participants made one pre-test baseline judgment for the position of the indicated finger. Stroking lasted 5 minutes per condition. Participants made one judgment per minute. Every one minute, tactile stimulation stopped, the lights under the two-way mirror were switched off to make the rubber hand invisible, and subjects were asked to make a judgment of the perceived location of the their finger. Other aspects of methods were the same as in Experiment 5-1. The experiment consisted of 12 conditions that were blocked, and randomly ordered between subjects.

Participants

Fourteen volunteers (mean age 26.5, 11 female) with normal or corrected to normal vision, all right-handed, gave their informed consent to participate in this study

5.1.3.2. Results

The mean raw judgment errors are shown in Figure 5-5 as a function of time. Judgment errors were calculated as the difference between the perceived and the real position of the participants' fingers. A positive error represents a mislocalization toward the rubber hand.

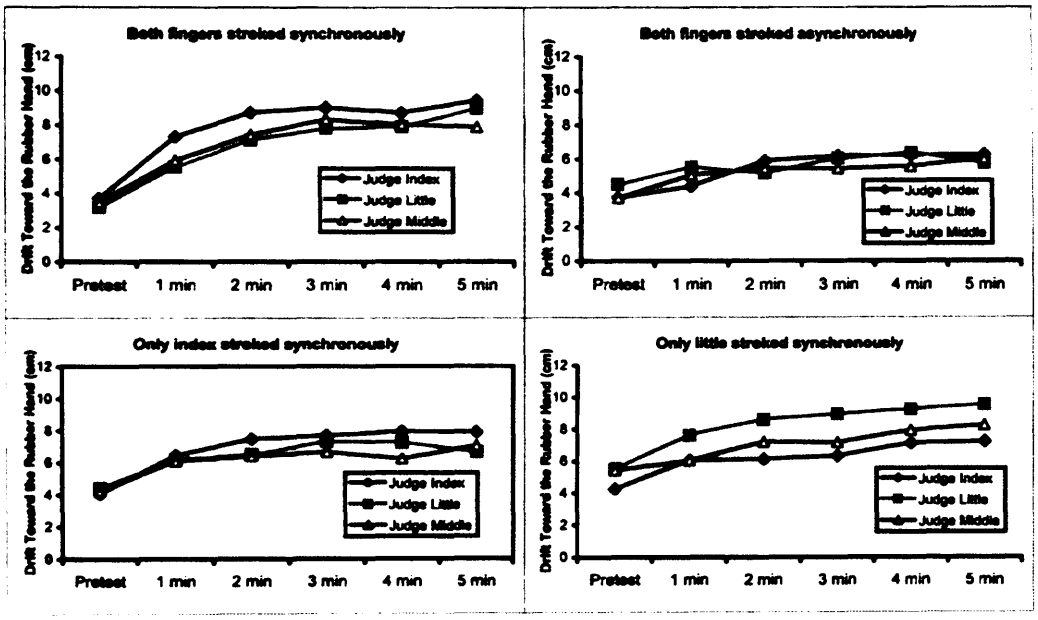

Figure 5-5. Mean raw judgment errors in the perceived position of each finger across time in Experiment 5-2. Participants made one pre-test judgment and then 4 judgments every 1-minute. Point "zero" represents the real position of the participant's hand.

Across all conditions, a positive judgment error was found even before stroking began. That is, subjects perceived their hand to be closer to the rubber hand than it truly was. For the synchronous conditions of stroking, the drifts towards the rubber hand were rapid, especially during the first 2 minutes. This suggests that the main effect of visuo-tactile integration was on the early portion of the curve. In asynchronous conditions, this early rise was reduced or absent. The mean judgment errors for the 5 judgements obtained during and after the stroking period were averaged and the baseline pre-test judgment was subtracted. The resulting proprioceptive drifts, calculated as the difference between the pre- and the post-test judgments were subjected to 2 separate analyses. The

first analysis focused on the investigation of the localized pattern of proprioceptive drifts. The second analysis focuses on the effect of the increase of tactile stimulation (two digits compared to one digit in Experiment 5.1) on the pattern of proprioceptive drifts.

Analysis I: Localized Proprioceptive Drifts

The first analysis investigated the localised effect of attribution. To investigate the local effect of visual-tactile correlation on the proprioceptive drift, a 2x2 ANOVA was performed on the mean proprioceptive drifts presented in Figure 5-6 with two within-subjects factors.

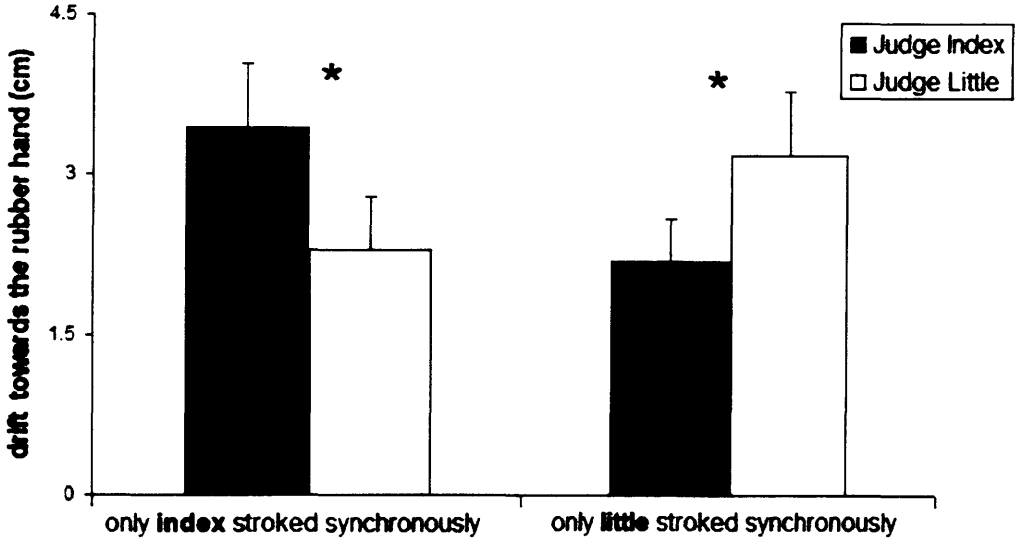

Figure 5-6. Mean proprioceptive drifts towards the rubber hand for the index and little fingers in Experiment 5-2. Error bars indicate standard errors. Point "zero" represents the felt position of the finger prior to stimulation. Asterisks indicate significant differences between judgments for the synchronously stimulated and the asynchronously stimulated finger. The crossover pattern of results replicates that of Experiment 5-1 (see Figure 5-2).

The factors were the mode of stroking (only the index synchronous vs. only the little synchronous) and the finger judged (index vs. little). Neither the main effect of mode of stroking ($F(1,13)= 0.144$, $p>0.05$), nor the main effect of finger judged ($F(1,13)=0.004$, $p>0.05$) were significant. But, the interaction between them was significant ($F(1,13)=5.26$, $p<0.05$). This interaction was observed because drifts towards the rubber hand were greatest when the finger judged was the one that was stroked

synchronously with the rubber finger, while the other finger was stroked asynchronously. Therefore, this crossover pattern of results replicates Experiment 5-2, with the additional control that all fingers received equal amount of stimulation in all conditions.

Analysis II: Is there a spatial spread of the proprioceptive drifts?

The second analysis focused on the spatial spread of attribution. A 2x3 ANOVA on the mean proprioceptive drifts presented in Figure 5-7, with two within-subjects factors was performed.

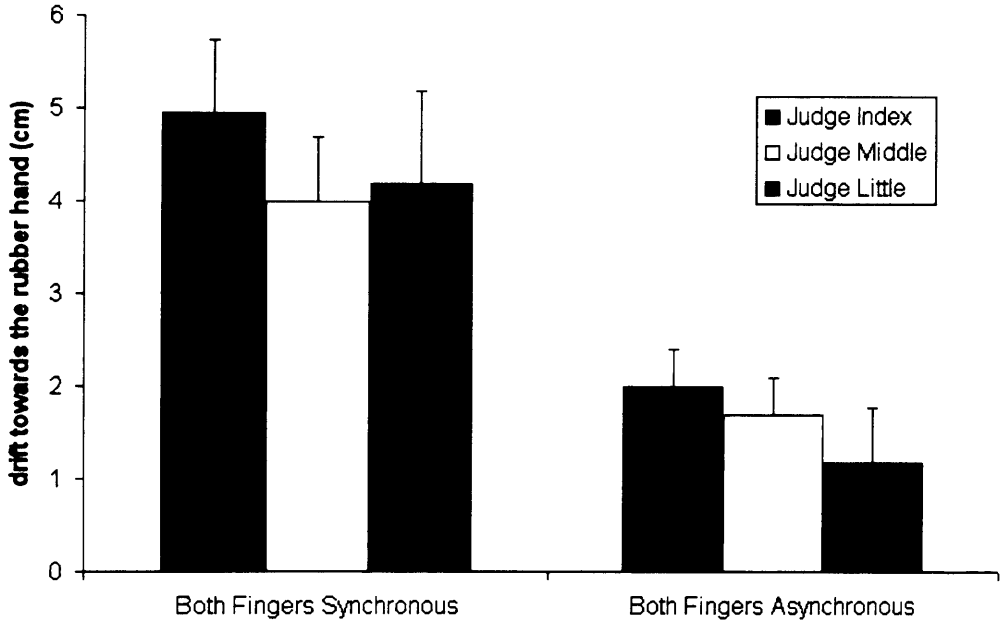

Figure 5-7. Mean proprioceptive drifts towards the rubber hand for the index, little and middle fingers in Experiment 5-2, when both index and little were stimulated synchronously or asynchronously. Error bars indicate standard errors.

The factors were the mode of stroking (both fingers synchronously vs. both fingers asynchronously) and the finger judged (index, little, middle). Only the main effect of mode of stroking was significant $F(1,13)=15.5$, $p<0.01$), whereas the main effect of finger judged was not significant ($F(2,26)=1.19$, $p>0.05$). The interaction of the two factors did not reach significance ($F(2,26)=0.832$, $p>0.05$). When both fingers were stimulated at the same time as the rubber fingers, then the unstimulated middle finger

drifted towards the rubber hand. The drift for the unstimulated middle finger was similar to those for the stimulated index and little fingers. A planned comparison for the judged position of the middle finger in the synchronous vs. asynchronous conditions confirmed that the RHI occurred in the absence of stimulation ($t(13)=3.32$, $p<0.01$, 2-tailed).

Taken together, these two analyses show that the RHI involves a partly fragmented body-awareness. First, proprioceptive drifts were greater for the finger that received synchronous stimulation with respect to the rubber hand, than for the finger that received asynchronous stimulation with respect to the rubber hand. However, when two fingers were stimulated synchronously with respect to the rubber fingers, the unstimulated finger (i.e. the middle finger) drifted to an equivalent extent.

5.1.4. Discussion of Experiments 5.1 and 5.2

In experiment 5.1, only the felt position of the stimulated finger drifted towards the rubber hand. Experiment 5.2 showed that even when two fingers received equal amount of stimulation, one synchronously and the other asynchronously, only the synchronously stimulated finger was felt to be significantly closer to the rubber hand, while no such drift was observed for the asynchronously stimulated finger. These findings suggest that synchronous visual and tactile correlation is a necessary condition for the inducement of the RHI. However, this pattern of localized proprioceptive drifts was not absolute. In experiment 5-2, the unstimulated middle finger drifted by an amount similar to the drift observed for the stimulated fingers, when both the stimulated fingers were synchronously stimulated. This pattern suggests that there is a spreading gradient of the RHI to unstimulated fingers.

It might be argued that the pattern of localized proprioceptive drifts reported in the present thesis provides support for the Bayesian approach, because stronger statistical correlations are expected only for the stimulated finger(s). The strong version of the Bayesian model postulates that the body scheme is constructed on the basis of visuo-tactile integration. The results of experiments 4.2 and 5.2 provide only partial support for the Bayesian account of localized proprioceptive drifts. This strong trend for localized drifts was restricted in two cases: first, the stimulated middle finger did not drift when subjects were looking at an incongruent rubber hand identity (Experiment 4.2, Chapter 4), and second, the unstimulated middle finger drifted to an equivalent extent when two fingers were stimulated synchronously (Experiment 5.2, present chapter). In Experiment 5.2, the unstimulated middle finger drifted more towards the rubber hand when the neighbouring fingers were stroked synchronously than asynchronously. A purely bottom-up account cannot explain how this effect was possible in the absence of stimulation. There seems to be a gradient of generalization of the illusion to the adjacent unstimulated fingers. This implies an influence of an additional non-visual representation of body-parts, which mediates the altered proprioception in the RHI. As shown in Experiments 4.2 and 5.1, the localized proprioceptive drifts can result from a purely bottom-up process related to the localized pattern of visuo-tactile stimulation, whereas the spreading pattern observed in Experiment 5.2 results from top-down influences. This paradigm

illustrates that the self-attribution of the rubber hand is neither a purely bottom-up effect, nor a purely top-down modulation.

This interpretation is compatible with a recent study by Braun and colleagues (2000) who showed that when participants were asked to discriminate stimulation on digits one and five, the distance between the cortical representations of the same digits, as measured by neuroelectric source localization of electroencephalograph, was increased compared with the passive stimulation conditions. However, Braun and colleagues also showed that finger representations in the primary somatosensory cortex are dynamically modulated by both top-down and bottom-up influences after prolonged durations of stimulation. Depending on the synchronous or asynchronous stimulation of multiple fingers, cortical representations of fingers can be either integrated or segregated (Braun et al., 2000; Braun et al., 2002a,b; Wang, Merzenich, Sameshima, & Jenkins, 1995). Braun and colleagues demonstrated that when participants were passively attending to the synchronous stimulation of digits one and five, the distance between the cortical representations of the two digits decreased as measured by neuroelectric source localization.

Overall, it seems that during the RHI, the body-awareness as measured by proprioception is partly fragmented. Only the finger that was synchronously stimulated was perceived to be significantly closer to the rubber hand across three experiments (Experiments 4.2, 5.1, 5.2). This fragmented pattern of localized proprioceptive drifts suggests that the sense of body ownership induced with the RHI can be generated quite locally, and involve individual stimulated body-parts. What can account for this pattern of fragmented proprioceptive awareness? The Rubber Hand Illusion is a purely passive experience, and to that extent it involves only afferent signals. Presumably, the localized proprioceptive drifts correspond to a highly localized activation of the somatotopical map of the stimulated body-part (e.g. finger). In fact, the somatotopical organization of the primary somatosensory cortex is highly segregated. The receptive field of neurons in SI corresponds to a small well-defined skin area. Neuroimaging studies confirm this orderly, segregated representation in human SI (Blakenburg et al., 2003). Therefore at the neural level, this pattern of localized proprioceptive awareness may reflect precisely the discrete somatotopy in SI. However, in everyday life proprioceptive awareness does not occur in isolation: almost always intermodal matching occurs within a dynamic and

active interaction between the agent and the environment, during which multimodal sensory and also motor signals need to be integrated. At the same time, a sense of the body as a coherent whole exists, but the Experiments 5.1 and 5.2 suggest that the coherence of the body-awareness may not be primarily sensory in its origins. To investigate whether body-awareness during action would be more global and coherent, Experiment 5.3 focused on the role of efferent information for body-awareness during a modified version of the RHI.

5.2. The Acting Self

5.2.1. Experiment 5.3

Experiment 5.3 was designed to assess whether action could alter the local and fragmented body-awareness induced with passive visuo-tactile stimulation during the RHI found in Experiments 5.1 and 5.2.

The bodily self involves two aspects that are normally confounded. These are the sense of agency and the sense of ownership (Gallagher, 2000a,b). Agency is the sense of intending and executing actions, including the feeling of controlling one's own body movements, and, through them, events in the external environment. Agency involves a strong efferent component, because centrally-generated motor commands precede voluntary movement. Ownership refers to the sense that one's own body is the source of sensations. The sense of ownership involves a strong afferent component, through the various peripheral signals that indicate the state of the body. Importantly, the sense of ownership is present not only during voluntary actions, but also during passive experience. In contrast, only voluntary actions produce a sense of agency. This asymmetry suggests that agency and ownership should have different effects on awareness of the body.

This hypothesis could be tested by applying a controlled, experimental method of manipulating body awareness, during active movements and passive stimulation. In the present context, body awareness refers to proprioceptive awareness, that is, the conscious experience of the location of a specific body-part (i.e. a finger or a hand) in space. The Rubber Hand Illusion offers one such method, because correlated visual and tactile inputs induce a changed awareness of one's body, which incorporates the rubber hand (Tsakiris & Haggard, 2005b).

As already shown, one consequence of the visuo-tactile correlation is that the proprioceptively-perceived position of one's own hand seems closer to the rubber hand than it really is (see Chapter 4). The RHI can thus be used to alter body awareness. Incorporation of the rubber hand into the body can be measured quantitatively via this drift in proprioceptively-perceived position. The present study compared the strength of

RHI induced by active and passive movement, to investigate the contributions of agency and ownership to body awareness.

The previous experiments (see Experiments 4.2, 5.1, and 5.2) suggested that body-awareness in the RHI is partly fragmented: only the finger that was synchronously stimulated was perceived to be significantly closer to the rubber hand. This fragmented pattern of localized proprioceptive drifts suggests that the sense of body ownership can be generated quite locally for individual stimulated body-parts. At the same time, a sense of the body as a coherent whole exists, both in everyday experience and in RHI experiments (see Chapter 4). Where might the coherence of the body scheme originate in the brain? Is it primarily the effect of sensory or motor processing?

The different principles of somatotopic organisation (Penfield & Boldrey, 1937) of the motor and sensory homunculus offer one approach to this question (see also de Vignemont, Tsakiris & Haggard, in press). The fragmented quality of body awareness measured in RHI experiments may reflect discrete somatotopic coding in S1. Conversely, representations of different body parts strongly overlap in the primary motor cortex (M1). It seems that MI is organized for representing muscle groups and movement synergies rather than individual muscles (Lemon, 1988). Control of single finger movement recruits a population of neurons distributed throughout MI, rather than a discrete group based on somatotopic organization (Schieber & Hibbard, 1993). These findings are consistent with the hierarchical control of synergies within the motor system. A task-level motor command (e.g. to grip an object) is expanded to produce synergic activation of muscles throughout the hand. Thus, in action, multiple body parts are controlled as an integrated whole.

Recent fMRI studies showing an overlap of activations evoked by different movements (Hlustik, 2001; Sanes et al., 1995) confirm this difference between motor and sensory somatotopy: "the somatotopy in SI is more discrete and segregated, in contrast to the more integrated and overlapping somatotopy in MI" (Hlustik et al., 2001, p. 319). If so, we might expect a less fragmented, more coherent version of the RHI for active (i.e. self-generated) movements than for purely sensory stimulation. For example, active movement of a single digit should produce general proprioceptive drifts for the whole hand, and not the localized proprioceptive drifts found after tactile stimulation.

To that extent, Experiment 5.3 compared the spread of the RHI from a stimulated finger to other fingers, after inducing RHI by three different kinds of stimulation. Subjects viewed a video-projected image of their hand, while they were actively or passively moving either their index or little finger. The active movement was self-generated, whereas the passive movement was passively-generated without any voluntary control by the participants. Comparing these conditions allowed us to disentangle agency and body-ownership. It was assumed that subjects acquire a sense of owning the projected hand in both active and passive conditions. However, they acquire a sense of agency over the projected hand in the active condition only. A third tactile stimulation condition was included for comparison with the Experiments 5.1 and 5.2. The video-projected hand was viewed either on-line (synchronous) or after a computer-controlled delay (asynchronous). Participants judged the proprioceptively-perceived location of the index or little finger.

Hypotheses:

1. Vision of both active and passive movements in the on-line synchronous condition would induce RHI, by analogy to previous tactile stimulation. Thus, the proprioceptive drifts after synchronous visual feedback will be significantly larger compared to the ones observed after asynchronous visual feedback.

2. The RHI effect (i.e. the proprioceptive drift) in the passive movement condition would be localised to the stimulated finger, whereas in the active movement condition, the perceived location of both the moved and unmoved fingers would drift to an equivalent extent. Efferent motor commands would be necessary for this spreading effect, because action would facilitate the integration and coherence of body representation.

5.2.2. Experimental Design & Methods

Design

The experimental design was 3x2x2x2 factorial.

Factor (i) had three blocked and counterbalanced levels: (a) tactile stimulation on a single finger by means of a paintbrush, (b) passive movement of a single finger generated by the experimenter, and (c) active movement of a single finger.

Other factors were:

(ii) the delay in the projection of the hand image (synchronous or asynchronous),

(iii) the finger stimulated (index vs. little), and

(iv) the finger whose position the subject judged (index vs. little).

All possible combinations of these three factors were performed in a different random order within each block defined by the first factor. The presentation of the first factor was counterbalanced across participants.

Methods

Participants sat in front of a table. At the beginning of each block, their right hand was placed by the experimenter at a fixed point inside a frame, whose upper surface, 180 mm above the table, was covered by a black screen. A video camera filmed the subject's right hand in first-person perspective. Black and white video images from the camera were captured, digitised on a computer and projected back onto the black surface, aligned with the midline (see Figure 5-8). The distance in the horizontal plane between the index finger of the subject's hand and its video projection was 15cm. All video projections involve some intrinsic delay: a calibration measurement of the system showed that the delay in the 'synchronous' condition was 100 ms. This is below the 150 ms value reported for detecting visuomotor delays (Franck et al., 2001; see also Blakemore, Frith & Wolpert, 1999). Indeed, debriefing of participants confirmed that they did not detect temporal discrepancy between touch and vision in the synchronous condition. In the asynchronous condition, an additional software delay of 567 ms was added to the video relay.

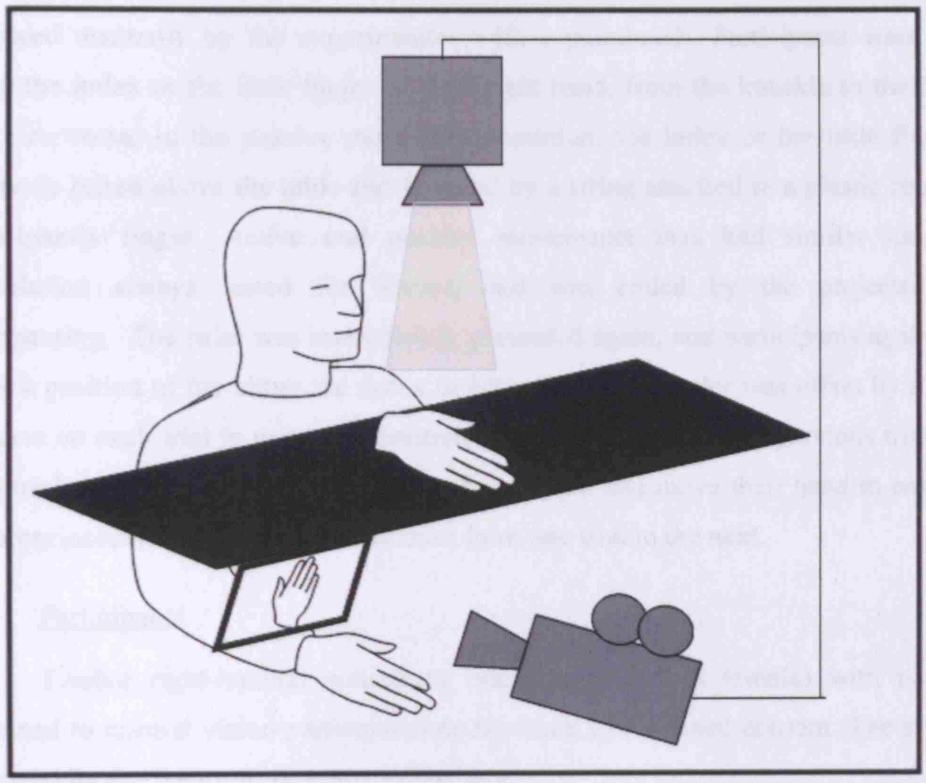

Figure 5-8 The experimental set-up in Experiment 5.3.

At the beginning of each block and before projecting the hand image, a pre-test baseline estimate of finger position was taken. Subjects saw a ruler presented in front of them on the black screen, 18cm above their resting hand. Participants were asked: "Where is your index/little finger?", and verbally reported a number on the ruler in response. They were instructed to judge the position of their finger by reporting the ruler number immediately above the centre of their fingertip. During the presentation of the ruler and while they were making the proprioceptive judgment, there was no tactile stimulation, nor movement of the finger. After the judgment, the ruler was removed, and the video image of the participant's hand was projected on the black screen, aligned with their midline.

In the active movement condition, participants were instructed to rise and lower their index or little finger while keeping the other fingers still. Participants were encouraged to alternate the rhythm (1Hz-2Hz) during the block, so that the movement was effortful and not repetitive. Participants received brief training in these rhythms

before the experiment. The experimenter stimulated using similar rhythms in tactile and passive movement conditions. In the tactile stimulation condition, stimulation was delivered manually by the experimenter with a paintbrush. Participants were stroked along the index or the little finger of their right hand, from the knuckle to the fingertip and vice versa. In the passive movement condition, the index or the little finger was passively raised above the table and lowered by a string attached to a plastic ring on the participant's finger. Active and passive movements thus had similar kinematics. Stimulation always lasted for 90secs, and was ended by the projected image disappearing. The ruler was immediately presented again, and participants again judged the felt position of the either the index or little finger. The ruler was offset by a random distance on each trial to prevent repetition of response values from previous trials. After each trial, participants were instructed to have a rest and move their hand to ensure that the proprioceptive drift did not carry over from one trial to the next.

Participants

Twelve right-handed volunteers (mean age 22.8, 8 female) with normal or corrected to normal vision participated on the basis of informed consent. The study was approved by the institutional ethics committee.

5.2.3. Results

A baseline pre-test judgment of hand position was obtained prior to stimulation/movement of the hand and a post-test judgment was obtained after the stimulation/movement. The pre-test baseline judgment errors were subtracted from the post-test judgment errors prior to analysis. We use the term "proprioceptive drift" for this change in the perceived position of the hand due to stimulation. Positive proprioceptive drifts represent a mislocalisation towards the projected hand image. Table 5-1 shows the mean and variability of proprioceptive drifts in each condition.

Table 5-1. Mean proprioceptive drifts in each condition for Experiment 5.3. Standard deviations across subjects are shown in parentheses. Positive drifts represent a drift towards the projected location of the finger.

		Tactile Stimulation		Passive Movement		Active Movement	
Finger Stimulated	**Finger Judged**	Synchronous	Asynchronous	Synchronous	Asynchronous	Synchronous	Asynchronous
Index	**Index**	3.25 (*1.86*)	0.58 (*1.83*)	3.25 (*2.17*)	1.12 (*2.30*)	2.50 (*1.60*)	2.00 (*1.12*)
Index	**Little**	0.83 (*2.48*)	-0.16 (*2.51*)	1.83 (*3.18*)	2.37 (*1.28*)	0.75 (*2.53*)	0.20 (*2.62*)
Little	**Index**	0.87 (*3.09*)	0.04 (*3.00*)	1.41 (*2.22*)	1.29 (*2.53*)	1.79 (*1.69*)	1.12 (*2.26*)
Little	**Little**	3.91 (*2.92*)	0.75 (*2.09*)	2.04 (*3.37*)	0.41 (*2.53*)	3.50 (*2.01*)	2.37 (*2.16*)
		**		*		*	
Marginal Mean Drift		2.21 (*1.33*)	0.30 (*1.14*)	2.13 (*1.93*)	1.30 (*1.39*)	2.13 (*1.24*)	1.42 (*0.99*)

The results were analysed in three ways. The first analysis assessed whether the three stimulation conditions did induce an RHI effect, by comparing the synchronous and asynchronous judgments for each mode of stimulation. The second analysis investigated whether the pattern of localized proprioceptive shifts observed in the previous experiments was present. Finally, a planned comparison was performed between active and passive conditions on the spread of the RHI measure across fingers, to investigate the effect of active movement on body-perception.

First, the statistical analysis investigated whether the video projection method induced a sense of owning the projected hand in each of the three stimulation conditions. To do this, the proprioceptive drifts obtained in the synchronous and asynchronous conditions were compared for each stimulation type, using a 3x2 within-subjects ANOVA. The first factor had three levels: (a) tactile stimulation, (b) passive movement, and (c) active movement. The second factor was the visual-tactile synchrony, which had two levels: (a) synchronous, and (b) asynchronous. Since the interest is in the overall level of the RHI, rather than its distribution across body parts, the data were pooled across all levels of the finger stimulation and finger judgement factors. The marginal means are shown in the last row of Table 5-1, and these means were submitted to the 3x2 ANOVA. There was no main effect of stimulation condition ($F(2,22)=1.051$, $p>0.05$). As predicted, the main effect of synchrony was significant ($F(1,11)=12.53$, $p<0.01$), because the proprioceptive drift towards the video image was greater following synchronous than asynchronous stimulation. The interaction of condition and synchrony did not quite reach significance ($F(2,22)=3.139$, $p=0.069$). The analysis confirmed the presence of RHI in each condition by using one-tailed planned comparisons. These showed greater proprioceptive drifts for synchronous than asynchronous conditions for all three types of stimulation (tactile $t(11)=3.96$, $p<.01$; passive $t(11)=1.803$, $p<.05$; active $t(11)=1.815$, $p<.05$). Thus, the basic RHI effect is found with a video image of the hand, and is induced by all three types of stimulation.

Second, the analysis considered whether the RHI in each stimulation condition was localised to the finger that was stimulated, or whether it transferred across fingers. To perform this analysis, the difference between synchronous and asynchronous stimulation effects on perceived position was calculated at each level of all other factors. This isolates the specific component of RHI due to synchrony of multisensory stimulation (see Chapter 4). The term "perceptual shifts" refers to this quantity. The perceptual shifts were calculated as the difference between the proprioceptive drifts observed after asynchronous conditions from the proprioceptive drifts observed after synchronous conditions. Figure 5-9 shows the mean perceptual shifts across conditions.

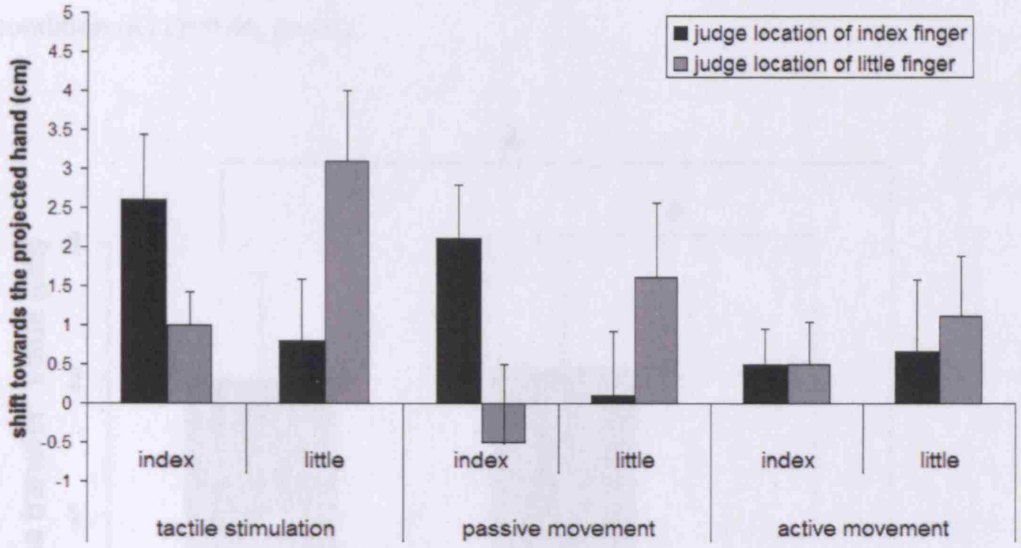

Figure 5-9. Mean perceptual shifts across conditions towards the projected hand. Error bars indicate standard errors. Point "zero" represents the felt position of the participant's finger prior to stimulation.

If the RHI is entirely localised, then the perceptual shift for a non-stimulated finger should be zero. If the RHI transfers fully from the stimulated finger to other non-stimulated fingers, then the perceptual shift should be equal for both fingers. Thus, a single "inverse transfer" quantity was defined that captures the spread of RHI across fingers, based on the above:

$$\text{mean}([(\text{Stimulate}_{\text{index}}\text{Judge}_{\text{index}}-\text{Stimulate}_{\text{index}}\text{Judge}_{\text{little}}),(\text{Stimulate}_{\text{little}}\text{Judge}_{\text{little}}-\text{Stimulate}_{\text{little}}\text{Judge}_{\text{index}})])$$

$\text{Stimulate}_{\text{little}}\text{Judge}_{\text{index}}$ refers to the perceptual shift in the perceived position of the index finger following stimulation of the little finger, and so on. This quantity represents the degree to which proprioceptive judgments for stimulated fingers differ from judgments for unstimulated fingers. High positive values of this measure occur when there are large shifts for the stimulated finger, and small shifts for the unstimulated one. This would imply a localised RHI which does not transfer across fingers. Perfect transfer across fingers would give a value of 0. The term "inverse transfer" is used for this measure. Figure 5-10 shows the mean inverse transfer values across conditions. Note that the "inverse transfer" measure is equivalent to quantifying the interaction between finger stimulated and finger judged for each type of stimulation shown in Figure

5-9. The inverse transfer measure was significantly greater than 0 in the tactile ($t(11)=2.52, p<.05$) and passive ($t(11)=2.37$, $p<.05$) conditions, but not in the active condition ($t(11)=0.46, p>.05$).

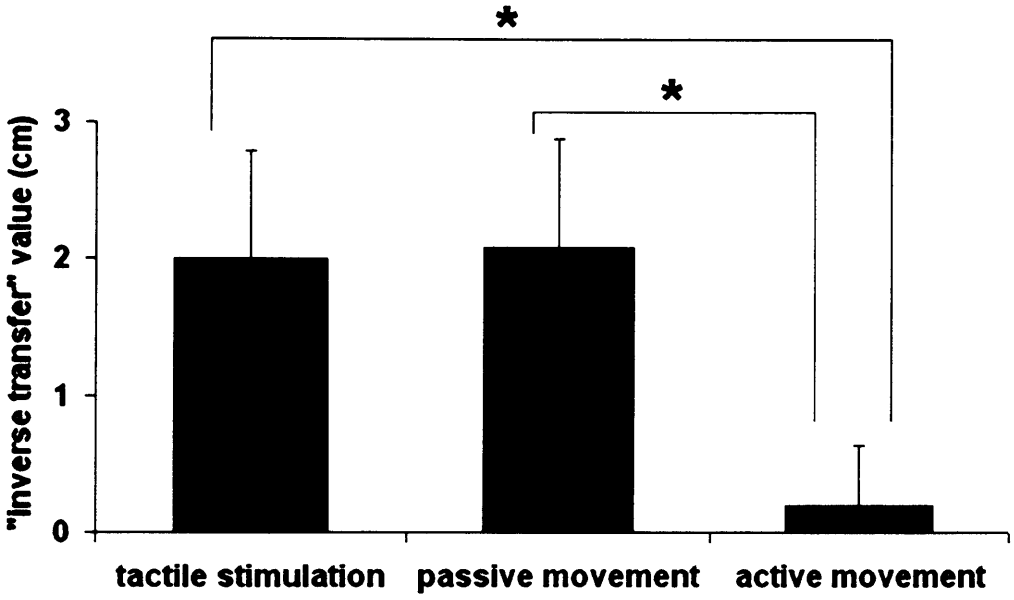

Figure 5-10. Mean "inverse transfer" measure across conditions. A high value indicates an RHI localised to the stimulated finger, while a low value indicates spread to unstimulated fingers. Error bars indicate standard errors. Asterisks indicate significant differences.

We had a priori hypotheses about the extent to which sense of agency and sense of ownership would involve localised body awareness. Specifically, it was predicted that active movement would induce a more coherent, less localised proprioceptive awareness than equivalent sensory stimulation. Thus, a directional planned comparison was performed to compare the inverse transfer measure following active movement with that following passive movement. The difference between active and passive conditions was significant ($t(11)=1.84$, $p<0.05$, one-tailed). This arose because perceptual shifts in the active, but not the passive condition, spread from the stimulated to the unstimulated finger. The difference between active movement and tactile stimulation were also significant ($t(11)=1.98$, $p<0.05$, one-tailed), for the same reason. Overall, these comparisons support the hypothesis that active movements would reduce the localized pattern of perceptual shifts reported in the Experiments 4.2, 5.1, and 5.2.

Control Experiment

The above results show that the sense of body ownership generated by voluntary action transfers well from one finger to another. Is this transfer a psychological feature of body representation, or simply a low-level motoric effect, due to the fact that moving a single finger requires widespread contraction of several muscles (Schieber & Hibbard, 1993)? A control experiment was performed to investigate whether spread of muscle activity from the moved finger to the other finger could underlie the observed pattern of results.

Subjects actively raised and lowered either their index or little finger in the same way as in the main experiment. Subjects were instructed to move their index or the little finger in different blocks, while trying to keep the other fingers still. They were asked to perform this active movement ten times with the index finger and ten times with the little finger. The order of blocks was counterbalanced. Subjects had direct vision of their hand. EMG was measured from the first dorsal interosseus (1DI) and from the abductor digiti minimi (ADM) of the right hand with bipolar recording from surface Ag/AgCl electrodes, amplified and digitised at 4 kHz. Four subjects (mean age 25.5, 4 female) participated in this control experiment after giving their informed consent.

The peak-to-valley EMG for each movement was calculated interactively, and the mean amplitudes were analysed using ANOVA. Figure 5-11 shows the mean peak-to-valley EMG amplitude across conditions.

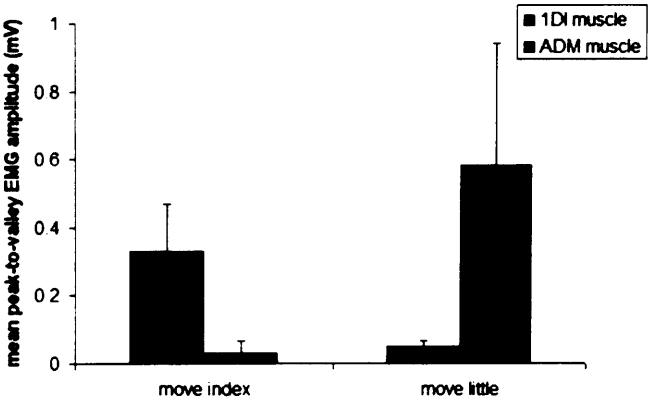

Figure 5-11. Mean peak-to-valley EMG amplitude measured from the 1DL and ADM muscles during active movement of the index or little finger. Error bars indicate standard deviations.

The mean EMG activity per subject per condition was submitted to a 2x2 ANOVA. The first factor was the finger moved (index or little), and the second factor was the muscle measured (1DI vs. ADM). The main effects were not significant ($F(1,3)=2.06$, $p>0.05$ for the finger moved, and $F(1,3)=1.44$, $p>0.05$ for the muscle measured). However, the interaction of the two factors was significant ($F(1,3)=40.54$, $p<0.01$) because active movement of one finger did not elicit a muscle contraction of the other finger. Thus, this control experiment showed that the movements studied were truly individual finger movements, whose control was essentially limited to the single intrinsic hand muscle acting as prime mover for that digit. There was no evidence for transfer or spread across fingers at the level of motor activity, ruling out a low-level motoric explanation of the inter-finger transfer of the sense of body ownership generated by active movement.

5.2.4 Agency Structures Body-ownership

Experiment 5.3 compared the influence of agency and sensory afference on body-awareness using a version of the Rubber Hand Illusion (RHI). In particular, a quantitative measurement of the RHI, namely a drift in the proprioceptively sensed position of one's own hand towards the rubber hand, was used to investigate the way efferent information influences the perception of one's own body.

A significant RHI effect was found in all three conditions, namely after tactile, passive and active stimulation. The manipulation of the video-projection of one's own hand induces a similar effect to the original RHI (see Chapters 4 and 5). Specifically, significantly larger proprioceptive drifts towards the video image occur after synchronous vs. asynchronous visual feedback, leading to a mislocalisation of the fingers. The results suggest that touch (tactile stimulation), proprioception (passive movement) and action (active movement), all constitute sources of bodily awareness.

However, the size of the RHI, measured as the difference in proprioceptive drift between synchronous and asynchronous conditions, was not constant. One surprise in this data was the high level of proprioceptive drift due to asynchronous active or passive movement. An artefact may explain why asynchronous active movement caused a very large drift. When people make active movements, the perceptual consequences of those actions are temporally attracted towards the action itself. This intentional binding effect (see Chapter 2, and Haggard, Clark & Kalogeras, 2002) would lead to asynchronous active movements being perceived as more synchronous than they really are. This would in turn increase their ability to induce an RHI. Turning to the passive movement condition, the high drift in the asynchronous condition may reflect the poor temporal resolution of proprioceptive information, which is known to be worse than the temporal resolution of efferent information (LaRue et al., 1995; Tsakiris et al., 2005). It is also possible that the reported proprioceptive bias towards the midline (de Graaf et al., 1995; Ghilardi, Gordon & Ghez, 1995; van Beers et al., 1995) interacted with the visual pattern of stimulation in an unknown way. However, these are post hoc explanations. Two points remain critical for the present experiment. First, the difference between synchronous and asynchronous conditions, and thus the RHI effect, was present for all

three types of stimulation. Second, this overall level of the RHI is logically independent of the spatial distribution of the RHI across stimulated and unstimulated fingers.

Having established the presence of the basic phenomenon of altered body awareness, the second analysis focused on how localised and finger-specific the observed phenomena were. The degree of localisation is a measure of body-unity, which can be compared across different stimulation conditions. Therefore, the focus was on the differences in the localised pattern of the RHI between these three sources of bodily awareness.

The pattern of localised perceptual shifts observed in Experiments 5.1 and 5.2 was replicated in the tactile stimulation and passive movement conditions of the present study. In the tactile condition, the perceived location of the stimulated finger shifted towards the video image location in the same way as in the original RHI. However, when participants judged the proprioceptive position of another finger which had not been stimulated, the shifts were significantly reduced. In the passive condition, a similar pattern was observed across fingers, even though the overall level of perceptual shifts was rather lower than in the tactile condition. The present results suggest that both touch and passive movement produce a relatively fragmented perception of one's own body, in which proprioceptive awareness is associated with individual body parts, and does not transfer to others. What can account for the similar pattern of shifts found in the tactile and passive movement conditions? These two conditions share a common characteristic, namely the absence of any active movement by the subject. Moreover, tactile and proprioceptive representations in the cortex show a similar somatotopic organisation, and many neurons respond to both cutaneous and proprioceptive inputs (Fitzgerald et al., 2004; Iwamura et al., 2002).

In the active movement condition, the proprioceptive drifts were lower overall than in the tactile and passive conditions. However, the proprioceptive drifts were statistically reliable, and moreover the differences between synchronous and asynchronous conditions (i.e. the perceptual shifts) were comparable to those observed in a passive condition that involved identical finger displacements. More importantly, the distribution of the perceptual shifts across fingers differed between active and passive conditions (see Figure 5-9). Passive movement stimulation induced perceptual shifts largely localised to the stimulated finger, with minimal transfer to the unstimulated

finger. Following active movement, in contrast, the proprioceptive judgments demonstrated a coherent representation of the hand, in which both the stimulated and unstimulated fingers showed proprioceptive positions shifted towards the video image. The "inverse transfer" measure for the active condition was not reliably above 0, confirming that the RHI spread across fingers. This contrasts with the fragmented proprioceptive awareness found during tactile stimulation and passive movement.

Could the spread of RHI in the active condition arise because moving one finger inevitably led to active contraction of other muscles too? Certainly, movements of individual digits can involve contraction of several muscles (Schieber, 1995). However, the control experiment suggests that in the paradigm used in the present study, active movement of the index finger did not involve contraction of the ADM muscle, and vice versa. That is, spread of activation between the index and little fingers did not occur at the muscular level. Studies of primary motor cortex coding have shown that single neurons may be activated during movement of any of a number of fingers (Schieber & Hibbard, 1993; for a review see Schieber, 2001), and the cortical territories associated with movements of the different fingers in man show considerable overlap (Hlustik et al., 2001). Thus, a distributed and overlapping population of central neurons may be involved in the individual finger movements studied here. This distributed coding of simple motor action may explain the spread of sense of ownership induced by action.

The fragmented pattern of proprioceptive shifts seen following tactile and passive stimulation, suggests that the proprioceptive sense of body-ownership is local. During voluntary action, the proprioceptive shifts were similar in size, but generalized across the whole hand. Therefore, the motor sense of agency influences the proprioceptive sense of ownership. This is compatible with Experiment 3.1, where differences in performance across conditions reflected a distinctive contribution of efferent information to self-recognition, and argued against a dominant role of proprioception in self-recognition. The functionally integrated control of action may have important consequences for subsequent body awareness, because action seems to produce a bodily coherence that is absent following passive movement.

6. Discussing the Bodily Self

6.1. Summary

The present thesis focused on the functional and phenomenal characterization of the bodily self. The bodily self was defined as a minimal sense of self, an embodied entity that produces sensory effects via its moving body. At the functional level, the bodily self is characterised by the generation of efferent signals and the reception of afferent signals. At the phenomenal level, the bodily self is experienced through the sense of agency wit respect to its own actions and the sense of ownership with respect to sensory events occurring in the physical body. Such motor and sensory events seem to be tagged as 'mine' in a way that exteroceptively-sensed events (e.g. sounds, lights) are not.

The methodological framework employed in the present thesis distinguished between two main aspects: the 'acting' and the 'sensory' self. This distinction allowed (i) the study of the bodily self in action, more specifically the distinct contribution of efferent information to the sense of agency and the sense of body-awareness, and (ii) the investigation of the functional and neural signatures of self-attribution and body-ownership in the sensory and the acting self. To that extent, the experiments reported in the present thesis employed various experimental paradigms and a series of depended variables that enabled the study of the bodily self.

The experimental studies presented in this thesis aimed at clarifying the interplay between central (i.e. efferent) and peripheral (i.e. afferent) signals for the sense of agency and body-ownership. In particular, the aim of the present thesis was twofold:

1. To investigate how agency modulates body-ownership, that is, to study the ways in which perception of one's own body is modulated by the intentional and agentic nature of voluntary actions.

2. To investigate the way in which multisensory signals, efferent signals and cognitive representations of the body are integrated to generate the sense of ownership over one's own body.

A brief summary of the main findings is presented below:

Time-awareness and somatosensory perception

The experiments presented in Chapter 2 investigated the role of efference for time-awareness and somatosensory perception. The results showed that both time-awareness and sensory awareness of self-generated somatic effects were modulated by the agentic nature of the action that caused them. In particular, the perceived time of a somatic effect was attracted to the perceived onset of the action that caused it, and the perceived time of the action was attracted to the perceived onset of the somatic effect. Similarly, the perceived intensity of the somatic effects is shifted: when the somatic effect was caused by a voluntary action, it was perceived as significantly less intense than when it followed a passive movement. This sensory suppression occurred in the absence of any precise prediction about the magnitude of the impending somatic effect. Overall, the results from Experiments 2.1 and 2.2 suggest that the efferent information is a critical element for the sense of agency.

Self-recognition

Experiment 3.1 investigated the specific role of efferent information for self-recognition. The results showed that voluntary actions significantly improved self-recognition judgments: self-recognition was significantly more accurate when subjects were themselves the authors of the action, even though visual and proprioceptive information always specified the same posture, and despite the fact that subjects judged the effect and not the action per se. The results suggest that proprioceptive self-consciousness may not be the kind of self-consciousness required for infallible self-recognition. Self-recognition, in the sense of correctly recognizing an external visual object or event as related to "me" seems to depend largely on efference and agency.

Self-attribution and body-ownership

The experiments presented in Chapter 4 focused on the functional and neural correlates of the Rubber Hand Illusion. The Rubber Hand Illusion offers one experimental paradigm that allows the manipulation of the sense of body-ownership. Overall, the results suggest that self-attribution of a body part, and hence body-ownership, arises as an interaction of bottom-up processes of multisensory integration and top-down influences originating from general body-scheme representations. At the neural level, the sense of body-ownership is associated with activity in the right posterior insula and and the right frontal operculum. Conversely, the sense of dis-ownership, that

is the sense that a body-part is not linked to the self is associated with increased activity in the left parietal cortex, in particular the primary and secondary somatosensory cortices.

Body-awareness of the sensory and the acting self

The experiments presented in Chapter 5 investigated (i) the effects of multisensory integration on proprioceptive awareness during the Rubber Hand Illusions, and (ii) the respective contributions of afferent and efferent signals to body-awareness during the illusion. Experiments 5.1 and 5.2 showed that proprioceptive awareness during the RHI is partly fragmented, because only the stimulated finger was perceived to be closer to the rubber hand than it really was. It was suggested that this effect might reflect the discrete and segregated somatotopical organization of the somatosensory cortex. It was then hypothesized that active movements, compared to passive sensory stimulation, would induce a more global and coherent form of proprioceptive awareness. This hypothesis was tested in Experiment 5.3, and the results confirmed the prediction that active, but not passive, movement induced a global change in proprioceptive awareness. Thus, active movements seem to integrate distinct body-parts into a coherent, unified awareness of the body.

6.2. Towards a Functional Characterisation of the Bodily Self

6.2.1. On Agency

The experience of the bodily self is linked to the sense of agency and the sense of body-ownership. These two "senses" are critically dependent on motor efferent signals and sensory afferent signals respectively. The present thesis attempted to show how these signals together generate the sense of agency and the sense of body-ownership, that is, by virtue of which sensory-motor processes actions and bodily effects are so clearly and inexorably experienced as "mine".

The sense of agency was defined as the sense of being the source of an action, that is, the sense of intending and executing an action (see Section 1.2.2). An agent is an intentional actor, whose behaviour is characterized by the presence of a reason (i.e. motive, desire, belief) to act in a way that will bring about the intended effect. Even though intentions seem to play an integral part of our conscious content of agency, their ontological status is highly problematic. The main argument against the causal role of intentions derives from the commitment of cognitive neurosciences to a form of physicalism that excludes the very possibility of mind-brain causation (see Libet, 1985). Moreover, because intentions seem to be closely linked to the sense of agency, it has been recently suggested that the sense of agency may in fact be a reconstructive illusion (Wegner, 2002).

However, the observation of human experience suggests that intentions form an integral part of our way of living and experiencing the world. In fact, it would be difficult to imagine how the human condition would be, if intentions did not really exist. Thus, even if cognitive neurosciences were to prove that intentions do not have causal power, or that the sense of agency is illusory, they would still need to account for their – perhaps only phenomenal- existence, not only in phenomenological terms, but also in functional and neural terms. To that extent, the cognitive neuroscience of agency should account for both the underlying brain processes, and also for the phenomenology of what it is to have an intention and act accordingly (i.e. to be an agent).

One first step towards the neuroscientific study of agency is to naturalize the phenomenology of action. This can become possible through the study of the

psychological consequences that the efferent and the afferent signals produce. The efferent and the afferent signals constitute the operation of the bodily self: through the efferent signals the self generates the intended actions, and through the afferent signals the self perceives its actions and the world. Thus, from a neuroscientific perspective, the emphasis on the role of motor and sensory signals that accompany every intentional voluntary action may provide a viable framework for the naturalization of intentional action (Tsakiris & Haggard, in press). In fact, it may be argued that any cognitive theory of voluntary action must start from a motor model of intentions, because at the ontological level, agency begins from our ability to move and control at will our bodies. A simple framework for a such a computational model has been presented in Chapter 3 (see Figure 3-10)

Searle's (1983) distinction between a "prior intention" and an "intention-in-action" can be of great use for the development of a motor model of intentions. A prior intention is defined as a mental planning of the action, and as such it represents the action as a whole (e.g. "I intend to submit my thesis tomorrow"). Prior intentions mark the beginning of the transaction that links cognitive representations to the physical events. The next step in this transaction is the formation of a specific intention-in-action. An intention-in-action represents the mental component that is internal to the action. According to Searle, the intention-in-action is almost contemporaneous with the agent's bodily movement (e.g. "I hand in my thesis"). This distinction is ecologically valid, because many of our everyday actions are experienced as being caused by intentions-in-actions, rather than by prior intentions (e.g. lighting up a cigarette). The reverse is not true. Whereas some actions are not caused by a prior intention, an intention-in-action precedes *every* action. In neuroscientific terms, the intention-in-action can be described as a specific motor plan, a motor intention that is in the process of being translated into muscle contraction. By decomposing intentions into prior intentions and intentions-in-action, cognitive neuroscience acquires a concept of intention that is neither too representationalist nor too detached from action itself.

The concept of efference copy is highly relevant to the idea of an intention-in-action or motor intention. Whenever a motor command is issued, a copy of this command is generated in parallel, and this copy is unique to voluntary actions. Accumulating evidence suggest that the efference copy is generated upstream of the

primary motor cortex. Supplementary motor area is probably one of the possible sources of the efference copy (see Deecke, 1987, 1996; Goldberg, 1985; Haggard & Magno; Haggard & Whitford, 2004; for a review see Tsakiris & Haggard, in press). One elegant demonstration of the role of SMA in the generation of an intention-in-action has been provided by Fried and colleagues (1991). Four epileptic patients reported an "urge" to move when they received direct electrical stimulation in SMA. Interestingly, higher current stimulation at the same site produced overt motor behaviour. Another example that illustrates the functional role of SMA for intentional action comes from the Anarchic Hand Syndrome. Patients with lesion in SMA and/or the carpus callosum (Della Sala et al., 1994) experience a rather unusual behaviour: their contralateral hand performs goad-directed movements, which were not consciously intended by the patients. It seems that lesion in the SMA may lead to a functional disconnection between the intention-in-action and the action itself, such that the patient does not experience agency over the movement of his affected hand.

Recent studies suggest that the efference copy is not simply a physiological signal used for motor behaviour. As shown by Blakemore and colleagues (2002) the processing of the efference copy within the motor system may also have important psychological consequences. Thus, the passivity experiences described by schizophrenic patients can be explained by a failure in the processing of the efference copy. Blakemore and colleagues write: "The patient with delusions of control is aware of his goal, of his intention to move and of his movement having occurred, but he is not aware of having initiated the movement." (Blakemore, Wolpert & Frith, 2002, p.240). The initiation of movement is linked to the generation of the efference copy, as this seems to be the primary signal that the central nervous system can use to indicate the generation of a descending motor command. As described in section 1.2.3, awareness of initiation of action seems to be related to neural processes prior to execution in the primary motor cortex (Haggard & Magno, 1999; for a similar view see Marcel, 2003). These observations seem to support the idea that efferent information is one critical link between the intention to act and the action itself. Therefore, the efference copy could also be used for generating the sense of agency (see also Haggard & Clark, 2003).

In fact, one implication of the experiments described in the present thesis is that the sense of agency seems to be closely linked to the efferent information. Two

functional signatures that characterize the sense of agency are the intentional binding and the sensory attenuation. Experiments 2.1 and 2.2 tested the hypothesis that agency is efferent-driven by investigating whether efference would be sufficient to elicit these mechanisms (i.e. intentional binding and sensory attenuation). In these two experiments, efference carried minimal information regarding the actual sensory effect. This "unusual" situation was created to ensure that any observed differences would reflect a genuine effect of the efferent information *per se,* and not an effect produced by the comparison between the prediction of the forward model and the actual sensory feedback. This efference copy can be termed "raw efference" because it contains minimal, yet critical temporal information for the link between the psychological and the physiological content of our actions. The results showed that this "raw" efferent signal is sufficient for eliciting both an intentional binding effect and a sensory attenuation effect. Importantly, efference acted as a general context for awareness, shifting perceived time and perceived intensity by fixed amounts. The fact that a "raw" efferent signals is sufficient for eliciting these effects suggests that the sense of agency arises as an efferent-driven predictive process. From a conceptual point of view, the efference copy is a pragmatic index of the ownership of movement that operates at the interface between the psychological and the physiological content of our actions. The psychological content is the intention-in-action, and the physiological content is given by the descending motor command and the sensory feedback.

Often philosophers remind neuroscientists that the concept of intention as used in many empirical studies may still betray some sort of commitment to dualistic traditions. One way of dealing with this paradox is to argue that intentions are ontologically bound to actual bodily movements. Schopenhauer (1969) denied the existence of volitions as mental willing, by replacing them with "acts of will" that are physical actions of the body. The act of will and the action is one and the same event that is given to the agent in two distinct ways: in an epistemologically immediate way as willing, and in a mediated way through the perceptual systems (e.g.vision, proprioception) as movement. The advantage of this view is that one can identify the bodily movement of a certain act with the psychological event of trying or willing to do this act (O' Shaughnessy, 2004). In that sense, intention or will is to be understood as "the activation of the motor-system that is blessed with the right psychological ancestors."(O' Shaughnessy, 2004,p. 208).

This "conceptual binding" of the intention to the actual action seems to avoid the dualistic concerns of both philosophers and neuroscientists. Interestingly, some of the neuroscientific data reviewed (see Section 1.3.1) and presented in this thesis (see Experiment 2.1, see also Haggard & Johnson, 2003) suggest that the awareness of intentions, actions and their effects are temporally bound to each other. This implies that the conscious experience of agency is an integrated and compressed version of the underlying neural events, in ways analogous to the philosophical prerequisite of an intention-action binding. In neuroscientific terms, it is by virtue of the generation of the efference copy that our bodily movements acquire the right psychological qualities that enable their characterization as agentic, because the presence of the efference copy denotes the origin of the action by tracing it back to the intention-in-action.

6.2.2 On Body-ownership

The phenomenology of agency is thin and elusive, whereas the phenomenology of the body is more salient. The phenomenal content of the bodily self is not linked so much to the sense of controlling the body (i.e. agency). Instead, the phenomenal content is given by the perception of explicit bodily sensations and of the effects of our own actions in the world. Importantly, the experience of the body seems to be linked to the self in a more immediate way than the experience of action. It is the sense of body-ownership that generates an explicit and immediate first personal perspective, probably because sensation has a more salient phenomenology than efference. Moreover, the sense of body-ownership is present not only during agentic actions, but also during involuntary movement, or at rest. It seems that agency represents something additional to ownership, but what? To answer this question agency has to be subtracted from an experimental measure of the bodily self, leaving the purely sensory sense of ownership. To that end, the present thesis distinguished between a "sensory" and an "acting" aspect of self-experience. This methodological distinction enabled the study of body-ownership in a purely sensory environment, and also the study of body-ownership during action.

The functional and neural correlates of sensory body-ownership were investigated in relation to self-recognition and self-attribution. In the absence of action, the body can be perceived only through afferent signals, some of which are thought to be ego-receptive (e.g. proprioception) and some of which are not (e.g. vision). These afferent signals need to be integrated in order to provide a unified percept of the body

and the world. The interactions between these signals have been at the centre of the neuroscientific research of self- and body-perception. Visual stimuli have predominated in this area, because ambiguities regarding visual representations of the body are both fairly convincing phenomenologically and also easy to produce via mirrors or virtual reality. This is the main reason behind the use of mirrors and video monitors in self-recognition experiments on dolphins (Reiss & Marino, 2001), chimpanzees (Kitchen, Denton, & Brent, 1996), infants (for a review, see Rochat & Striano, 2000), and adults (for a review, see Jeannerod, 2003). For example, the manipulation of the visual feedback of one's own hand or the visual presentation of a rubber hand can create a situation of conflict between the afferent signals. These manipulations allow the investigation of the interplay between vision and proprioception or vision and touch and its effect on body-ownership.

The experiments presented on self-recognition and self-attribution (see Chapters 3, 4 and 5) showed that proprioceptive information can be overridden or altered to produce an "erroneous" sense of self. For example, when subjects experience a passive movement of their own hand, while they are looking at someone else's hand moving in a similar way, they wrongly recognize the moving hand as being theirs. Likewise, when subjects see a rubber hand being stroked synchronously with their own unseen hand, it is as if their own tactile sensation is caused by the paintbrush touching the rubber hand and not their own hand. The effect of this visuo-tactile integration is an alteration in the proprioceptively sensed location of their hand. These results seem to suggest that intermodal matching is not only a necessary but also a sufficient condition for self-attribution, and hence body-ownership. Consequently, any object can become part of *me*, simply because strong statistical correlations between different sensory modalities are both necessary and sufficient conditions for self-attribution. On this view, psychological concepts such as embodiment and selfhood are unnecessary, because purely Bayesian principles of statistical correlation are sufficient to extend the body representation, to include even body parts as implausible as tables (Armel & Ramachandran, 2003).

However, not all objects are experienced as being part of my body, simply because in some cases there is no functional reason for an external object to be part of me. For example, in one experiment (see Experiment 4.1), when subjects were looking at a neutral object being stroked with a paintbrush synchronously with respect to their own

hand, the visuo-tactile correlation did not induce a change in the perceived location of their own hand towards the viewed object, suggesting that the neutral object was not attributed to the self (cf. Armel & Ramachandran, 2003). It is possible though that once this neural object has to be used by the body (e.g. a tool), then it will become a "bodily auxiliary, an extension of the bodily synthesis" (Merleau-Ponty, 1962, p152), and it will cease to be simply an external object (see Iriki Tanaka & Iwamura, 1996).

Interestingly, when subjects saw a neutral object being stimulated synchronously with their own hand (see Experiment 4.1), the induced proprioceptive shifts were in an opposite direction, namely away from the neutral object. This "perceptual repulsion" might reflect a behavioral correlate of the dissociation between events that either do or do not produce self-attribution. Interestingly, this effect is compatible with the results of Experiment 2.1 on time-awareness. In that study, the results showed a perceptual attraction between one's own action and an external consequence, and a perceptual repulsion for a physically comparable involuntary movement followed by the identical external consequence. It seems that in both body representation and intentional action, perceptual attraction seems to be the hallmark of the bodily self, while perceptual repulsion may be characteristic of events not linked to the bodily self.

Consequently, whereas afferent signals can be used to induce an extended sense of ownership, this sense is still bodily in its core, meaning that it should correspond to the way the body is represented in the brain. This view assumes that there is a pre-existing representation of the body to which the new object is incorporated. The concept of body schema is relevant here because its functional role is to constrain the multisensory integrations in a way that guarantees the spatial and structural coherence of the body. Thus, the rubber hand or any other object that will be self-attributed as a result of the synchronous visuo-tactile stimulation has to be functionally compatible with the representation of the "body in the brain".

As shown in Chapter 4, three factors originating from body-schema representations seem to constrain the effects of intermodal matching: body-specificity, anatomical constraints, and body-part identity. The viewed object has to be a body-part, and not a neutral object that has no functional connection with the body (see Experiment 4.1). The body-part has to be in a posture that is anatomical plausible and congruent with the posture of the subject's own body-part (see Experiment 4.1), and of the same identity

as the subject's stimulated body part (Experiment 4.2). These top-down constrains on body-related multisensory percepts suggest that self-attribution, and hence, body-ownership is not a purely bottom-up process driven only by afferent signals. In addition, body-ownership cannot be simply a purely top-down process driven by abstract cognitive body-representations, because that would not explain how an attribution process of an external object is possible at all. Instead, body-ownership seems to arise as an *interaction* between bottom-up processes originating from the "body in the world" (i.e. multisensory perception) and top-down influences originating from the "body in the brain" (i.e. body representations). The synchronized visual and tactile stimulation causes the illusion, but the phenomenological effect within the illusion is a description of one's own body, and not a description of the stimulation.

The distinction between the causes of the RHI and its phenomenal effect at the psychophysical level was also used to investigate the neural correlates of the causes and the effect of body-ownership. Regarding the neural *causes* of body-ownership (see Experiment 4.3), it was shown that a distributed neural network is involved in the processing of the multisensory signals and in detecting the congruency between them. In particular, the posterior part of area BA44 was involved in detecting discrepancies between visual, tactile and proprioceptive bodily-related signals, while the right posterior cortex and in particular the right SII was involved in the processing of selective discrepant features of body-specific stimulation, such as the asynchronicity between visual and tactile percepts. When the integration of the multisensory signals failed to induce a sense of body-ownership, activity was observed in the left somatosensory cortex. The functional role of the somatosensory cortex could be in signalling the current state of the pre-existing body or in maintaining a stored reference frame of the body against conflicting sensory signals which cannot be assimilated to the pre-existing body. It is also possible that the observed activity in the somatosensory cortex can be explained by back-projections originating from the parietal (Schaefer et al., 2005b,c) and the premotor cortices (Ehrsson et al., 2004).

With regards to the neural signatures of the experience of body-ownership, a strong correlation between activity in the right posterior insula and frontal operculum and the strength of the illusion as measured by proprioceptive drift was found. The observed activity in the posterior insula is interesting because the same area has been

implicated in action-recognition (see Farrer et al., 2003a). The fact that, in the present study, activity in the insula was also found in the absence of movement implies that this area may in fact reflect body-ownership, and not agency.

This conclusion is compatible with the idea that agency represents something additional to body-ownership, but it also shows that it is particular difficult to dissociate agency from body- ownership. Most studies of agency reveal a brain network which heavily overlaps with the body ownership network (se Berti et al., 2005; Karnath, Baier & Nagele, 2005). One interpretation of this fact would be that in the voluntary movement of our bodies we continuously demarcate the limits of our body. One approach that has been put forward in the present thesis was the selective manipulation of efference, while afference was maintained constant. In this way, the content of body-ownership (i.e. the afferent signals) would be, in principle, similar across conditions, but the context within which these signals were generated would be different. This approach was used to investigate the way agency interacts with body-ownership to generate a coherent experience of the bodily self.

6.2.3. On Agency *and* Body-ownership

Recent work on self-consciousness has argued that highly abstract cognitive representations, such as the 'self', may be understood in terms of their sensory-motor bases (Bermúdez, Marcel & Eilan, 1995; Roessler & Eilan, 2003). By abandoning the strict dichotomy between perception and action, between sensory and motor functions, cognitive neuroscience was faced with the task to account for a pre-reflective form of consciousness, a primitive bodily self-awareness. Interestingly, two different, sometimes opposed, philosophical traditions contributed significantly towards this direction. Analytical philosophy of mind, possibly for the first time, recognized the necessity to account for the intrinsic relation between the body and the self (Bermúdez, 1998; Bermúdez, Marcel & Eilan, 1998). On the other hand, phenomenology has long advocated the corporeal nature of cognition, but it is only recently that the work of Husserl and Merleau-Ponty can be discussed in a naturalistic neuroscientific perspective (Gallagher, 1997; Gallagher & Varela, 2001; Petitot, Varela, Pachoud & Roy, 1999). Interestingly, analytical models of body-awareness emphasize proprioception as the constitutive element of the bodily self, whereas phenomenological models stress the primacy of movement in constituting embodied agency (Sheets-Johnstone, 1999).

One current analytical view holds that proprioception is a primitive form of self-consciousness (Bermúdez, 1998). The experimental studies presented in this thesis suggest that purely afferent information can produce an "anomalous" bodily self, in the sense that the subject can mis-attribute someone else's hand or a rubber hand to herself. The present thesis also shows that self-generated movements produce a different kind of body awareness than purely afferent signals.

The experiment on self-recognition presented in Chapter 3 specifically addressed the role of agency for body-ownership. As predicted, a voluntary action significantly improved the self-recognition performance. In the absence of efferent information, congruent visual and proprioceptive feedback, as is the case in the RHI, led to a self-attribution of an alien moving hand. Overall, the results showed that efferent information clearly contributes to the ability to match proprioceptive and visual representations of a remote bodily effect. One interpretation of these results focused on the precise temporal information that efference carries with it. This temporal signal can be used to predict the onset of the movement and also the arrival the impending somatic effect. On another view, the forward model could have contributed to the matching process by generating accurate kinematic predictions. Experiment 3.1 did not dissociate between these two alternatives, and a follow-up experiment is required to answer whether a purely temporal efferent signal would suffice for accurate self-recognition.

The effect of agency on body-ownership was also assessed in a modified version of the RHI. One surprising finding was that body-awareness during the RHI is partly fragmented. Only the finger that was synchronously stimulated was perceived to be significantly closer to the rubber hand across three experiments. This pattern of localized proprioceptive drifts reflects a fragmented body-awareness during purely sensory conditions. The localized proprioceptive drifts suggest that the sense of body ownership can be generated quite locally for individual stimulated body-parts. One explanation put forward was that the fragmented proprioceptive awareness may reflect the orderly and segregated somatotopical representation in the sensory cortex. Given that efference produces a more coherent self-representation as shown in the self-recognition experiment, it was hypothesized that voluntary actions should reverse the pattern of localized proprioceptive drifts, by spreading the effect to the whole hand. Localized proprioceptive drifts, specific to the stimulated finger, were found after tactile

stimulation and passive movement. Conversely, during active movement of a single digit, the proprioceptive shifts were not localized to that digit, but were spread across the whole hand. Whereas a purely proprioceptive sense of body-ownership is local and fragmented, the motor sense of agency integrates distinct body-parts into a coherent, unified awareness of the body.

In the self-recognition experiment, the movements were confined to one finger, and had minimal spatial detail. Self-generated actions provided a precise temporal signal which could be used to predict proprioceptive and/or visual feedback. In Experiment 5.3 the difference between action and passive movement was studied in an off-line, rather than an immediate test, using a spatial rather than a temporal measure. Taken together, the observed differences between active and passive conditions reflect a distinctive contribution of efferent information to both *temporal* and *spatial* aspects of body awareness.

Thus, it is suggested that agency is critical for the coherence of body ownership. Sensory mechanisms generate a sense of ownership based on fragmented local representation of individual body parts, but action provides a coherent sense of bodily self. It seems that the unity of bodily self-consciousness comes from action, and not from sensation, because the active body is experienced as more coherent and unified than the passive body. Since unity and coherence are key features of self-consciousness (Kant, 1881/1996), it is suggested that action plays an important role in the sense of self, over and above that of afference. Other studies have also shown an efferent benefit for proprioceptive precision (Paillard & Brouchon, 1968), for somatosensory prediction (Blakemore, Wolpert & Frith, 1998), and for action-recognition (Knoblich & Flach, 2001; Knoblich, Seigerschmidt, Flach, & Prinz, 2002). The present thesis suggests to the extent that the self is coherent, this coherence comes from efference and not from afference.

Overall, the bodily self seems to be constituted by voluntary movement, and it is experienced as a "perspectival source" (Gallagher & Marcel, 1999; Marcel, 2003) that modulates the phenomenal experience of peripheral and central signals. The results presented in this thesis suggest that the sense of agency is efferent-driven, whereas the contents of body-ownership are predominantly afferent in their origins. The contents of body awareness are also modulated by cognitive body representations that preserve the

coherence of the "body in the brain". In addition, efference intrinsically modulates the perception of one's one body by generating a coherent representation of the "body in action". This effect of efference is not surprising since in general we actively explore our environment, rather than passively perceiving it. In this sense, body awareness is not simply another form of object consciousness. Models of self-awareness based on the idea that proprioception is the privileged "sense of the self " ignore the mere fact that my body is not so much an object of perception, but rather it is given to me as a subject, and that agency actually structures the experience of my bodily self.

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